
THE FOSSIL RECORD OF ANGIOSPERMS: REQUIEM OR RENAISSANCE?¹

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ABSTRACT

The fossil record of angiosperms has more potential than ever for contributing to the resolution of major questions in the evolution of the flowering plants due to the better understanding of the significance of leaf and pollen records and because of the increasingly complete and informative fossil record of flowers. Nonetheless, the record has fallen short of its potential (and of its potentially synergistic value) because, although it is better understood than ever, there are still problems in identifying fossils' affinities that have not been fully resolved and that have major implications with respect to determining timing in angiosperm evolution with either molecular clock-based models or minimum-age node mapping. This issue is of particular significance with respect to early angiosperm radiation, where more careful studies of existing specimens seem to have unrealized value for increasing our comprehension of floral evolution and homology, potentially in the context of strides in understanding MADS-box genes. Subjective methods with typological overtones are still often used in identifying fossils, even though phylogenetic context is available. Identification using phylogenetic context, among other things, does not obscure relative character changes within monophyletic groups, does not lend itself to facultative interpretation of affinities to suit outcomes of various models, and, thus, does not impede our understanding of angiosperm evolutionary history. Nonetheless, a reasonably good fossil record of angiosperms is emerging from the combined efforts of many laboratories and, when carefully evaluated, reveals an interesting and possibly informative pattern of flowering plant evolution. One of its most striking aspects is the rapid radiation of angiosperm taxa that are now unusually diverse around two particular times in geological history: the Turonian and Early Tertiary. Possible reasons for these intervals of rapid radiation among angiosperms will be discussed.

Key words: Cretaceous, diversification, Hymenoptera, insect pollination, MADS box, molecular clock, Tertiary, typological.

As the post-genomics era unfolds, the role of the fossil record in addressing broad questions related to plant evolution has come under scrutiny. While there are certain aspects of fossil data that are unique and cannot be replaced by comparative studies of extant taxa, the primacy of fossil evidence in what have been key areas exclusive to the domain of paleontology has been challenged. For example, the implications of fossil evidence in timing evolution, one of the principal areas of its importance, has often come into conflict with predictions derived from molecular clock-based models that sometimes produce dramatically contrasting results (Wikström et al., 2001; Crepet et al., 2004; Graur & Martin, 2004; Sanderson et al., 2004). In these latter instances, the fossil record's flaws are often invoked directly or by implication to explain the discrepancies in favor of the model's results (Burnham, 2008), or there may be a tendency to look too hard for fossils that might corroborate the predictions of such models with the danger that standards of identification might be

relaxed in so doing (Crepet et al., 2004). Another manifestation of conflicts between the results of molecular-based models and the fossil record involves dramatic examples where the taxonomic affinities assigned to fossil taxa have been reinterpreted because of conflicts with predictions based on models, despite the uncertainties associated with the models themselves and without supporting analyses that might favor the suggested change in affinities (Nixon, 2008). These instances reveal trends that could diminish the impact of fossil evidence in the face of alternative methodologies before the potential value of fossil evidence is fully realized and before the accuracy of such alternative means of timing has been fully evaluated. With the possibility of controversy in such a critical area as timing, the full potential of fossil evidence in understanding evolutionary history cannot be appreciated because the potential informative value of plant fossil data depends on correlative studies that, in turn, depend on timing (i.e., models explaining evolutionary events can be evaluated for

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consistency with the fossil record) or on paleobiogeographic/paleoecological context that, again, requires an accurate time frame. This paper is one in a collection of symposium contributions aimed at examining the fossil record of plants to illustrate how it might continue to be of value in the face of dramatic new developments in molecular genetics and their applications (e.g., Downie & Palmer, 1992; Parkinson et al., 1999; Chaw et al., 2000), and at providing examples of new applications of fossil data in this context. Due to obvious space limitations, it is by no means a comprehensive treatment of all aspects of the integration of fossil and modern data, but is intended to underscore the importance of fossils and their unrealized potential at a time when excitement generated by alternative, powerful techniques may obscure the value of fossil data and ultimately diminish its contributions to addressing questions of interest and importance. This would eventually have the ironic result of limiting the impact of important breakthroughs in molecular genetics by removing a valuable set of tools from interpreting and using such approaches.

Certainly, the fossil record does have uncontested and exclusive domain in its potential for revealing taxonomic history in an ecological or a paleobiogeographic context. Thus, the fossil record empowers an entire class of studies of evolution/development where, in addition to timing and relationships, ecological context is also important for understanding evolution (e.g., Jablonski, 2005). While studies of molecular genetics have the potential to illuminate key events in evolution by identifying genes and clarifying genetic control mechanisms associated with timing in development (in addition to the taxonomic distribution of these genes), critical aspects of the relationship between evolution and development would be invisible to studies that focused exclusively on contemporary species (e.g., correlations between environment or key environmental components [s.l.] and character innovations [e.g., Crepet, 2000; Grimaldi & Engel, 2005; Jablonski, 2005; Labandeira, 2006]). Thus, separate from its historical importance in attaining our present understanding of the history and evolution of life, the fossil record has unique properties that are important to a deeper understanding of evolution depending on the nature of the particular fossil record and how it has been interpreted and applied.

THE FOSSIL RECORD

VALUE OF FOSSIL EVIDENCE

The fossil record provides information relevant to understanding plant evolution and diversity in a

number of important areas including the following: (1) Determining the pattern of taxa appearances through time—this allows tests for consistency with various evolutionary ecological hypotheses via comparisons with hypothesized related parallel events. (2) Determining minimum times of appearance of characters or taxa—especially important in the context of depositional environment. (3) Identifying morphoclines—transitional states that form a sequence linking two disparate homologous conditions where transitional types may be difficult to hypothesize (verifiable in phylogenetic context). (4) Identifying mosaics or links among taxa, such as extinct taxa that include combinations of characteristics now found in different taxonomic groups and, therefore, are possibly useful in linking groups (i.e., missing links through the combination) or in checking existing phylogenies for consistency (i.e., if the combination of characters verified in a fossil taxon cannot occur on a phylogenetic tree, then that tree is incorrect). These taxa, as informative as they might be, are invisible in cases where typologists, baffled by their unique nature, attempt to identify them without including them in phylogenetic context. This approach has obscured the observation of evolution within lineages and opens the door for controversy about affinities by making determinations necessarily, to at least some degree, subjective. (5) Observing distribution changes through time, allowing for a check on paleobiogeography patterns and their implications for explaining modern distributions (Raven & Axelrod, 1974). (6) Reconstructing paleoecology/climatology. (7) Examining the evolutionary implications of depositional environments. (8) Identifying extinct diversity. (9) Observing adaptive radiations and mass extinctions (e.g., turnover rates).

As implied above, the plant fossil record, which includes only morphology and structure with very occasionally preserved chemistry, might be considered one of two independent sets of data relevant to plant history, evolution, and relationships. The other is based on extant taxa and includes comparative morphology, structure, and molecular genetics data. With respect to analyzing the significance of these separate sets of data, complementarities now exist in various combinations of fossil and modern data through phylogenetic analyses, in assessments of congruence checks between fossil mosaics and phylogenies generated without fossils, by comparisons between apparent character transformations based on fossil intermediates and those implied by phylogenetic context or even by underlying molecular genetics, and by general comparisons between patterns based on comparative analysis of extant taxa with their implied sequences of evolution and patterns observed in fossil

history. Analyses that include some synthesis between these data sets aimed at understanding evolution have changed progressively with the development of new methodologies in phylogenetic analysis (e.g., Nixon, 1999, 2003) and advances in molecular genetics. There are, however, enduring first principles upon which effective interpretations of fossil data depend. The most fundamental of these is accuracy in identification of the fossils (Gandolfo et al., 2008). Without such accuracy, none of the potential of fossil taxa can be realized. Timing, a critical example, follows from the pattern of appearance of taxa that are accurately identified. This pattern in time has enormous value beyond simply determining minimum times of appearance of taxa or characters or as references for molecular clock-based models (Crepet, 1996; Magallón et al., 1999; Crepet et al., 2004; Friis et al., 2006).

IDENTIFICATION OF FOSSIL TAXA

With respect to maximizing the potential informative value of the fossil record in any of the areas mentioned above (or in any of its usual applications), it is the seemingly simple and straightforward process of taxon identification that has caused a great deal of controversy in interpreting the fossil record of plants, particularly, but not exclusively, angiosperms, and has also prevented the full realization of the potential informative value of the plant fossil record. For vascular plants, the fossil record is further complicated by the fact that entire organisms in reproductive state are seldom preserved with component organs in organic connection. Often, only some parts of particular taxa are known as fossils. This phenomenon (i.e., that of missing morphological/structural characters) has significant implications for the identification of fossil taxa that are the foundation for other inferences and insights that may be derived from fossil evidence in the areas noted above (Nixon & Davis, 1991; Nixon, 1996). The potential associated with a pattern of evolution of taxa set in chronology and ecological context cannot be realized unless fossil identifications are precisely accurate or precisely as accurate as possible because affinities based on subsets of characters are, after all, only best estimates.

Reliable identification of fossils is more important than ever in light of widely accepted phylogenies based on molecular data that imply a sequence in timing (relative appearances) due to their hierarchical nature (i.e., creating a possible subliminal tendency to look for what might be expected in the fossil record as mentioned above). Facultative interpretations of fossils' affinities, easier to do with less rigorous methodologies for fossil taxon identification and

inspired, whether subliminally or not, by phylogenies based on molecular sequence data, would be harmful to the scientific method because such interpretations might effectively eliminate the independence of fossil evidence as a corroborative instrument by linking expectations to outcomes in the realm of identities. Thus, the significance of the fossil record would be diminished, and the test for congruence between two independent sources of data, which should ideally strengthen our understanding of evolutionary history, would be compromised. Proof against this eventuality would be a careful, open methodology for taxonomic affinity determination—a methodology that, ideally, might take into consideration and compensate for challenges in describing and classifying fossil taxa whose character associations reflect evolutionary change (that is, those different from their closest modern relatives). In other words, a methodology that would allow for precise placement of extinct taxa.

PHYLOGENETICS AND IDENTIFICATION

Cladistics or phylogenetics has made it possible to identify fossils through placement in phylogenetic context (e.g., Donoghue et al., 1989; Nixon, 1996). Thus, affinities of extinct taxa may be identified precisely and with objectivity, even though they would be difficult to determine through comparisons of tables of characters in cases where the fossil taxon's characters do not exactly correspond to the characters found in any possible modern relatives. In addition, the evolutionary significance of such fossils can be evaluated as changes in character-complements within monophyletic groups, which can be tracked because relationships among these fossil taxa are revealed through phylogenetic context. Phylogenetic context also focuses investigators on taxon-defining synapomorphies.

IDENTIFICATION METHODOLOGIES: HISTORICAL PERSPECTIVE

Previous to and leading up to the advent of phylogenetic methodology, there has been an evolution of identifying methodologies throughout the 20th century that is perhaps most easily illustrated in angiosperm paleobotany. One can posit that the evolution of identifying methodologies began with the criterion of general similarity in what were considered taxon-defining characters and, in the absence of phylogenetic methodology, proceeded to what has amounted to an essentially typological method of identification involving gross character comparisons via tables. The latter approach, initiated in response to the need for a more objective identification methodology, has been used historically

in conjunction with increasingly rigorous standards for describing fossils. While not ideal, it is still sometimes employed despite the fact that the weaknesses of such an approach are now obvious (by depending on congruence of character associations for taxonomic placement, the approach cannot deal effectively with extinct taxa characterized by unique combinations of characters without subjective interpretation). In essence, this method could result in shoehorning fossil taxa into particular extant groupings defined by strict character associations (typology). This methodology obscures the evolutionary process by denying or minimally, by obscuring, one of its fundamental aspects—character association changes. This tabular character-matching method then, by necessity, also involves subjective assessments of affinities in cases (most depending on the taxonomic level and age of the fossil taxon in question) where the match is imperfect. Thus, these methods have limited the impact of fossil evidence in plants, particularly in angiosperms, given that entire suites of characters are usually not available for analysis.

In contrast, phylogenetic context provides an alternative methodology for identifying extinct taxa that do not precisely conform to the character complexes now found in their closest modern relatives (e.g., Herendeen & Crane, 1992; Crepet & Nixon, 1998b). In addition to representing an optimal means of placing fossil taxa, precision identification through phylogenetic analysis is also the best way to cope with inevitable differences of opinion that characterize the scientific community by reducing the level of subjectivity inherent in other methodologies. These are inevitable in the face of the limited numbers of characters available in fossils and, frustratingly, often involve fossils of unusual potential significance. Nonetheless, such disputes, while relatively common and potentially distracting, are important correlates of the scientific method and, if conducted within the boundaries of phylogenetic methodology, are resolvable within the limits of the relevant fossil evidence. Indeed, phylogenetic context is the only reasonable method for resolving such differences because alternatives represent a regress to methods abandoned years ago by systematists because of the well-known flaws in fundamentally subjective approaches (e.g., angiosperm systematics in 1960), and, to reiterate, determination of affinities by comparisons of characters through tables is inherently subjective because there is no logical way to deal with incongruities that are the norm and not the exception when dealing with fossils (at any but the higher, and often less informative or relevant, taxonomic levels).

TWO CASE STUDIES: CRETACEOUS MONOCOT FLOWERS AND AN EARLY CRETACEOUS ANGIOSPERM

There are many examples of differences of opinion on the affinities of important fossils. Two, in particular, are appropriate in the context of this paper: (1) reports of certain Cretaceous monocot flowers and (2) reports of a unique Early Cretaceous angiosperm. These illustrate the differences between what might be characterized as subjectively based disagreements on affinities and ones founded on conflicting results of alternative phylogenetic analyses.

The monocot example is a case of a challenge to an assignment of affinities involving a number of Cretaceous taxa, exemplified by *Mabelia* Gandolfo, Nixon & Crepet (Gandolfo et al., 2002; Figs. 2A, B, 10A), that have been placed with modern Triuridaceae on the basis of phylogenetic analysis. Although the triuridaceous affinities have been effectively universally accepted by monocot specialists (e.g., Chase, 2004) and experts in modern Triuridaceae (e.g., Rudall, 2003) on the basis of phylogenetic placement of these fossils, Friis et al. (2006) question such affinities. Their challenge is based on differences in pollen morphology between the one modern taxon of Triuridaceae for which pollen morphology is known and the fossil taxa, and on the presence of a staminal column in one of the fossil taxa. They consider the staminal column found in some of these fossil taxa as a more generally ANITA clade dicot character (Friis et al., 2006) and not one found in modern Triuridaceae. In fact, the character assemblage of the fossil triuridaceous taxon *Mabelia* reflects remarkable congruence with those of taxa found in the modern family Triuridaceae (Gandolfo et al., 2002). However, its pollen is monosulcate and, thus, more generalized than the monosulcate-derived pollen found in the only modern taxon of Triuridaceae (out of 34) for which pollen has been described (Furness et al., 2002). Furthermore, staminal columns are actually well known in the modern family Triuridaceae (Maas & Rubsamen, 1986: fig. 14h; Maas, 1988: figs. 3, 10a). Suggestions of alternative affinities with more generalized ANITA dicots have not been supported by an evaluation/criticism of the original matrix of Gandolfo et al. (2002) on which triuridacean affinities have been assigned. Thus, this difference in interpretation by Friis et al. (2006) does not include, nor is it based on, a contravening phylogenetic analysis that would support the assertion that the fossil has more generalized non-triurid affinities (Friis et al., 2006). In the absence of an alternative analysis based on accurate characterization of modern and fossil characters, assertions of alternative affinities become subjective and an extension of the character-matching

or phenetic approach used widely before phylogenetics was available. The difference in interpretation seems based on only the alleged incongruence in characters between the fossil and modern taxa. These alleged instances of incongruence are misplaced given that at least one of the characters actually does occur in modern triurids and that the pollen differences, considering their nature and the severely limited extent to which pollen morphology is known in modern members of Triuridaceae (i.e., similar pollen could ultimately be found to exist among the 33 taxa of living triurids for which pollen morphology is now unknown), are in any case consistent with generally accepted trends in pollen evolution as well as with the well-documented tendency for pollen morphology to temporally lag floral morphology as documented in numerous Cretaceous taxa (see Friis et al., 1994; Zhou et al., 2001; Hermsen et al., 2003; Crepet et al., 2004). Just as original identifications of fossils via this method of character matching have been historically difficult because they do not accommodate evolutionary change within (monophyletic) lineages, criticisms of this type are similarly based on methodologies that do not allow for the possibility of differing rates of evolution among characters found in particular clades. So, in this case, according to the criteria suggested by Friis et al. (2006), pollen would have had to evolve at the same rate as the other floral characters in order for the fossils to be defined as triurids (also assuming that no monosulcate pollen types will be found in any of the 33 species of extant triurids for which pollen is now unknown). In this regard, it is striking that some orchids might not be defined as orchids under such a methodology because they have monads or tetrads instead of polyads (Pacini & Hesse, 2002).

A good example of a disagreement on affinities taking place within the framework of phylogenetic analysis is the Lower Cretaceous fossil taxon *Archaeofructus* Sun, Dilcher, Zheng & Zhou, a fossil with implications as to early angiosperm floral morphology and perhaps to the origin of flowers (Figs. 1A, B, 8A). It is an unusual angiosperm, having naked, unisexual reproductive structures that are apparently not organized in flowers, with affinities either to all of the angiosperms (Sun et al., 1998, 2002) or, with a different interpretation of the reproductive organs as secondarily simple due to reduction, to the Nymphaeales (Friis et al., 2003). This difference of opinion has taken place entirely within the context of phylogenetic analysis (compare Sun et al., 2002 and Friis et al., 2003). The challenge to the original placement of *Archaeofructus* at the base of all other angiosperms was based on a reanalysis of the Sun et al. (2002) matrix following the addition of another existing nymphaeoid taxon *Cabomba* Aubl. (Friis et

al., 2003). The methodology was explicit and can be objectively evaluated. It happens that there was an error in coding leaf characters in Cabombaceae in the Friis et al. (2003) paper (Cabombaceae were coded as having dissected leaves when, actually, they have both dissected submerged leaves and entire-margined floating leaves; Nixon, 2006). When corrected and the modified matrix reanalyzed, there is no support for the inclusion of *Archaeofructus* within Nymphaeales (Nixon, 2006). While this particular challenge to the affinities of a fossil taxon may have been based, at least partially, on a coding error, the point is that the explicit nature of phylogenetic context allowed for an evaluation of the original identification by peers and also permitted an evaluation of the criticism. This is a good example of a healthy difference of opinion that is supported by critical evaluation, just as the original identification was supported by such evaluation. Nonetheless, the issue of affinities of *Archaeofructus* is not fully resolved. Limited numbers of characters are known for the fossil taxon, keeping its actual affinities controversial. Recent assertions that some of the reproductive branches of similar, presumably closely related taxa bear both carpels and stamens (an interpretation that would make the reproductive branches inflorescences) complicate the issue (Ji et al., 2004). However, this interpretation is not convincingly supported by the illustrations purporting to reveal such bisexual fertile axes, which seem instead to reflect several layers of plant organs compressed together. This is an important issue that can only be resolved through further empirical study of the fossils in question followed by critical analysis. It focuses on the importance of first principles in paleobotanical studies (i.e., that the fossil taxon's characters should be explicitly understood and clearly demonstrable based on the study of the fossil).

BROADER RELEVANCE TO ANGIOSPERMS

The issues above play out in important ways that are current with respect to a set of evolutionary mysteries that hold a commanding position among those concerning plant history. The circumstances surrounding the radiation of angiosperms comprise some of the most addressed and notably unresolved questions in plant evolution. There have been numerous articles on the many facets of angiosperm evolution, and many of these have contributed to our understanding of the questions associated with angiosperm history. These questions include: (1) ancestry—still famously unresolved with underlying homologies (to be revealed by molecular genetics studies or by yet-to-be discovered fossil evidence) being key to its resolution, and its correlate, the origin

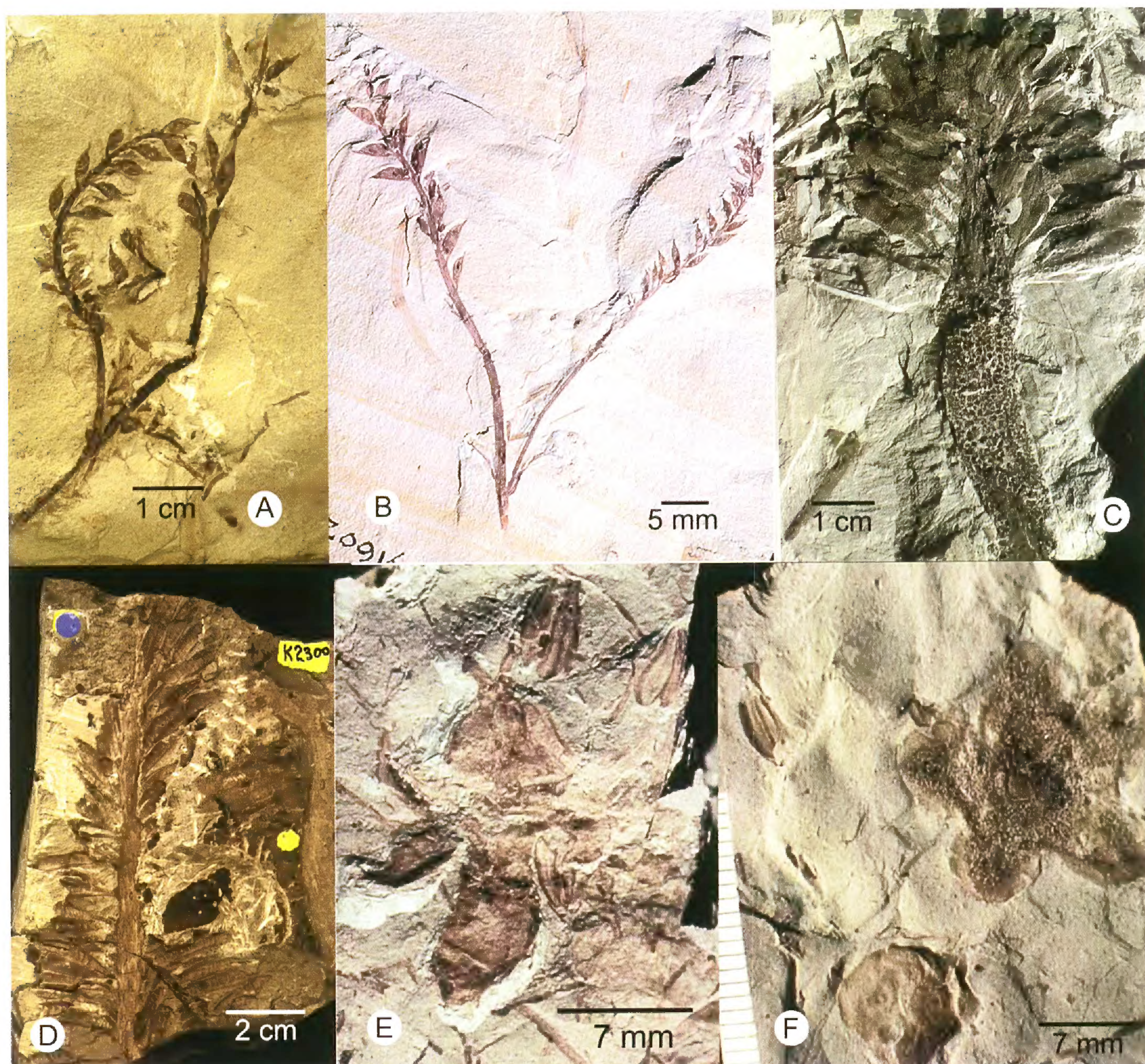


Figure 1. A, B. *Archaeofructus* fertile branches (Nanjing Institute of Geology and Paleontology collection numbers SZ0917 and SZ0916). —A. Note that stamens subtend carpels on the branch on the left, and that while the fertile branches are subtended by bracts, there are no bracts or obvious floral envelope parts subtending the carpels or stamens along the fertile axes. —C, D. *Archaeanthus* Dilcher & Crane (University of Florida collection numbers UF15706-3084 and UF15703-2300); fruits from the Cenomanian of Kansas, U.S.A. Mature carpels are helically arranged on elongate axes. E, F. Compressed dicot flowers from Rose Creek, Nebraska. —E. Note stamens and carpels with separate styles and stigmas (UF15703-4026). —F. Note the radial symmetry and the apparent nectary ring and partitions separating the carpels (UF15713-3429). A–F with permission of D. L. Dilcher, Florida Natural History Museum.

of angiosperm-defining characters in ecological context; (2) within angiosperm relationships—long problematic due to convergence and homology problems and now the domain of molecular systematics (a possible escape route from convergence issues but perhaps one not yet fully resolved); (3) the dramatic rise of angiosperms to numerical species dominance and possible reasons for it; and (4) the history of angiosperm distribution patterns. There is a great deal of enthusiasm about the prospects for homology resolution in the area of molecular genetics (e.g., Theissen et al., 2000, etc.), especially given that morphological intermediates may never have actually

existed, which might account for the difficulty in identifying angiosperm outgroups.

These questions have been addressed using new applications of fossil evidence. New analytical methods continue to provide hope that they will be successfully resolved. In posing the question as to how the potential of fossil evidence may be realized with respect to angiosperm history, it should again be kept in mind that reliable and appropriate fossil evidence is required, i.e., the identifications and ages of fossils must be accurately determined, and, likewise, the nature of the fossil evidence must be appropriate to the questions being addressed (e.g., questions regard-

ing flowers for evolution of pollination). In addition, methodologies must appropriately compensate for weaknesses in the fossil record (an area itself that is subject to question) in, for example, timing (minimum age node mapping or molecular clock-based models) or in phylogenetic placement of the fossils.

With respect to the questions above, it is interesting to review changing approaches to the study of angiosperm fossils because the fossil record has fallen short in some areas. One of the issues affecting our understanding of angiosperm evolution in historical context has been the unreliability of the fossil record. Studies of angiosperm fossils have been plagued by poor identification methodologies and limited by the incomplete nature of the fossil record. Nonetheless, there has been a historical trend toward increasingly rigorous methods for angiosperm fossil identifications resulting in what has now become a much more informative fossil record. With respect to angiosperm fossil identification, an important revolution of sorts was already underway in the late 1960s. New criteria were being applied in the identification of angiosperm leaves by Hickey (1971), Dilcher (1974), and Hickey and Wolfe (1975), while Doyle (1969), building on the careful stratigraphic palynology of Brenner (1963) and employing careful pollen character analysis developed with Walker (Walker & Doyle, 1975), LeThomas (1981), and others, began a comprehensive look at angiosperm pollen radiation (see also Muller, 1981). Thus, the groundwork was being laid for a better understanding of angiosperm history, an area of considerable confusion prior to that time because of rampant misinterpretations of angiosperm fossils that often erred in the direction of assigning modern affinities to fossils where such assignments were unwarranted. And, as noted above, methodologies evolved to include careful comparisons of character complexes that were more reliable than previous methods but that have aforementioned limitations in the face of better approaches afforded by phylogenetic context. With respect to the incomplete nature of the fossil record, phylogenetics and minimum age node mapping provide a means of filling in gaps as do various molecular clock-based models for determining timing.

THE VALUE OF FLOWERS

Given that the background of extensive leaf and pollen records and their increasing value as criteria for fossil identifications have become more rigorous, the advent and continuing investigations of fossil flowers have added significant critical mass to the angiosperm fossil record. Furthermore, flowers add several important dimensions to the record. They embody many taxon-defining characters and reveal

aspects of past angiosperm reproductive biology, an aspect of angiosperms that has often been invoked to explain their relative success (Grant, 1949; Raven, 1977; Regal, 1977; Burger, 1981; Crepet, 1984; Crepet & Friis, 1987; Friis & Crepet, 1987; Eriksson & Bremer, 1992). A great deal of hope has been associated with the prospect of the recovery of a reasonably accurate fossil record of flowers as a remarkable flower record has been unfolding. While historically sporadic studies of fossil flowers have been a characteristic of angiosperm paleobotany (e.g., Conwentz, 1886), sustained efforts to find and describe fossil flowers began with investigations of compressed Tertiary flowers (e.g., Crepet et al., 1974, 1975; Crepet & Dilcher, 1977; Crepet & Daghighian, 1980; Crepet & Taylor, 1985, 1986; Crepet & Nixon, 1989a, b), followed in short order by investigations of lower Middle and Late Cretaceous fossils, represented by a variety of preservational modes (Dilcher et al., 1976; Tiffney, 1977; Basinger & Dilcher, 1984; Crane & Dilcher, 1984; Dilcher & Crane, 1984; Crepet & Friis, 1987; Friis & Crepet, 1987; Crepet & Herendeen, 1992; Crepet et al., 2004; Friis et al., 2006). As a result, a pattern of evolution of flowers has now emerged that can be reviewed with the fossil records of other plant organs as well as fossil insects that are potential pollination vectors. This collective "biotic" approach can provide insights into the evolution of reproductive biology in the angiosperms. In addition, this record of flowers, in the contexts of the carefully vetted leaf, fruit, and pollen records, provides a comprehensive record of angiosperms that can be compared to the hypothetical sequences of taxon appearances implied by phylogenies based on extant taxa and to hypotheses of timing in angiosperm history derived from various molecular clock-based models (e.g., Crepet et al., 2004). In addition, the flower record provides insights into the evolution of pollination mechanisms in angiosperm history and further illuminates relative rates of evolution among different plant organs, thus increasing the value of the fossil records of dispersed non-floral organs. This kind of information also provides insights into angiosperm reproductive strategies during key periods during their diversification.

TIMING ANGIOSPERM HISTORY

An important aspect of interpreting the significance of the history of the angiosperm fossil record and one that was once an uncritically accepted correlate of that record is the timing implied by it. Insights into questions that may be addressed by fossil evidence depend on correlation consistency with various ecological/evolutionary hypotheses, distributional

changes (Tiffney, 2008), and character evolution and its significance, and these depend on accurate timing. While timing is implied by the fossil record, the fossil record is far from perfect, and assessing the accuracy of timing implied by the fossil record in the context of molecular clock-based models has become an interesting, important, yet controversial issue (see Crepet et al., 2004; Sanderson et al., 2004; Nixon, 2008). There are a number of approaches to determining timing with fossil data. First are direct inferences from raw fossil data (i.e., data accepted from literature), second are inferences from the carefully screened (for reliability) fossil record, and finally, inferences based on various models, notably minimum age node mapping or molecular clock-based models. Of course, each of these approaches has strengths and weaknesses (e.g., uncritically evaluated literature can be misleading, critically evaluated literature may leave gaps in taxon histories, and models fill in gaps, but methodologies are in transition and their reliability controversial), but whatever the methodology employed, a more accurate and complete fossil record would and will enhance our understanding of timing. Thus, even with respect to establishing accurate timing, and in the face of a radically improved fossil record of angiosperms, the major questions surrounding angiosperm history are only partially resolved.

THE FOSSIL RECORD OF ANGIOSPERMS

In light of the discussion above, a review of the carefully vetted fossil record of angiosperms (i.e., fossils found to have synapomorphic characters defining the taxa to which they have been assigned or to have had their affinities determined directly in the context of phylogenetic analyses) that integrates new discoveries does reveal some interesting aspects of their history that have relevance to major unresolved issues in angiosperm evolution. There has been a recent analysis of the fossil angiosperms based on the criteria of synapomorphy or phylogenetic context (Crepet et al., 2004) and also a more recent review of the fossil record of angiosperms (Friis et al., 2006) that takes these criteria into account to some degree in its summary of angiosperm history. Friis et al. (2006) also raise a number of issues worthy of discussion, and these will be or have been considered throughout this paper (e.g., monocot fossil record, etc.). The following discussion of the angiosperm record (taxon appearances and character appearances) is based principally on flowers but is congruent with other fossil organs as noted in the relevant discussions. This discussion incorporates results of earlier reviews of the early fossil record of angiosperms.

There is emphasis on Turonian (89–93.5 million years ago [Ma]) and younger angiosperm fossils in the context of the earlier fossil record of angiosperms as summarized and discussed in previous papers (Friis et al., 1986, 1997; Crepet et al., 2004; Friis et al., 2006). Key Early Cretaceous taxa, however, are discussed at length in the contexts of the overall fossil record of flowering plants and of the Turonian reports (when these are deemed to be more reliable evidence than the earlier reports of the same taxa) and how they have been investigated.

IMPORTANCE OF THE FOSSIL FLOWER RECORD OF THE TURONIAN

As with new floral evidence from all Cretaceous and Tertiary intervals, Turonian data have supplied a wealth of information of angiosperm history and, given generally accepted patterns of angiosperm diversification, represent the angiosperms at an important moment in their history. These fossils are remarkable for their quality of preservation (e.g., Staedler et al., 2007) and document surprising diversity in angiosperms at a relatively early time (depending on the taxon). In addition, they reveal that certain characters and taxa had yet to evolve. These Turonian fossils include numerous initial appearances, changing our view of timing in angiosperm history in significant ways, especially with regard to the rosid-asterid radiation and also, more broadly, with respect to adaptations for insect pollination.

TIMING: EARLIEST EVIDENCE OF TAXA AND CHARACTERS REPRESENTED BY TURONIAN FOSSILS

The following taxa appear first in Turonian deposits (consistent with the Angiosperm Phylogeny Group [APG] II system except as noted): Nymphaeaceae s. str., Monocot megafossils, putative Magnoliales, Caryophyllales, Hamamelidaceae, Altingiaceae, Hydrangeaceae, Iteaceae, Fagales, Rosaceae, Brassicales, Malpighiales (Clusiaceae), Myrtales, Melastomataceae, and Ericales (Ericaceae) (Crepet et al., 2004).

THE FOSSIL EVIDENCE

NYMPHAEACEAE

The Nymphaeaceae comprise an interesting family placed at the base of angiosperms by molecular systematics analyses and reported based on leaves and other flowers from other sediments including sediments earlier than Turonian deposits (Friis et al., 2001, 2006). The fossil record of Nymphaeaceae is unsettled in the sense that there is some level of

controversy around each of the reports of nymphaeaceous flowers and inflorescences. The possibility that an unusual nymphaeaceous taxon is represented by *Archaeofructus* (Fig. 1A, B) has been discussed above, and it is too controversial to include this taxon in the fossil record of Nymphaeaceae. More plausible reports of Nymphaeaceae are based on mesofossil evidence that includes a putative flower of Nymphaeaceae from 100 Ma sediments of the Early Cretaceous (Friis et al., 2001). However, its assignment to Nymphaeaceae s. str. does not withstand rigorous phylogenetic analysis using the same matrix employed by Friis et al. (2001; adapted from Les et al., 1999) and including only those characters available in the fossil as opposed to those inferred characters figured by Friis et al. (2001; Gandolfo et al., 2004). Upon phylogenetic analysis using the Les et al. (1999) matrix originally employed by Friis et al. (2001), results indicate that affinities are equally compatible with Illiciaceae as well as with other angiosperm families, suggesting that *Microvictoria* Gandolfo, Nixon & Crepet (Figs. 2C, D, 10B), described by Gandolfo et al. (2004), is the only unequivocally strictly nymphaeaceous fossil from the Early Cretaceous. Nonetheless, the putative nymphaeaceous fossil taxon described by Friis et al. (2001) has significant implications that are relevant to the age of Nymphaeaceae because of its equal compatibility with Illiciaceae, which suggests the node that includes both Nymphaeales and Illiciales can be dated at 113 Ma which is consistent with phylogenetic analyses (Crepet et al., 2004; Friis et al., 2006). Thus, the fossil nymphaeaceous taxon *Microvictoria*, while the earliest confirmed record, probably does not reflect the actual age of the family, which is projected at least 113 Ma by minimum age node mapping (Crepet et al., 2004).

Another perspective on the age of Nymphaeaceae that challenges both reports is derived from application of molecular clock-based models (Yoo et al., 2005). The challenge is based not on the morphology of fossils, but on the fact that they dramatically alter the outcomes of model-based angiosperm dating if they are included as calibration points (Yoo et al., 2005). The conflict with model-based analyses brings up issues involving the accuracy of the applications of at least some of these models and is discussed in detail in Nixon (2008).

MONOCOTYLEDONS

Flowers of Turonian-age Triuridaceae have already been discussed above. They exist in the context of an interesting, relatively sporadic, and somewhat controversial fossil record. Based on minimum age node mapping, Crepet et al. (2004) projected an origin for

monocots of no later than 98 Ma, consistent with some model-based projections (Magallón & Sanderson, 2002). Despite the projections of an Early Cretaceous origin, the accuracy of the Lower Cretaceous fossil record of monocots (Doyle, 1973) has recently been challenged (Gandolfo et al., 1998, 2000; Crepet et al., 2004), but a recent report of distinctive pollen of Araceae may provide valid Lower Cretaceous evidence of the monocots (Friis et al., 2004). With respect to traditionally cited monocot fossils of Early Cretaceous age, Gandolfo et al. (2000) make the case that the common Early Cretaceous angiosperm fossils, leaves, and pollen are not sufficiently divergent from basal ANITA clade dicots in characters that have been preserved to allow their unequivocal identification as monocot remains. With respect to dispersed palynomorphs, it is not clear that monosulcate pollen with reticulate micromorphology and a gradient in lumina size is restricted to monocots or even to angiosperms (Zavada, 1984).

Monocots from the Cretaceous (Turonian) are represented by what are generally agreed to be flowers representing Triuridaceae (see discussion above; Figs. 2A, B, 10A), a family of saprophytes with very simple and presumably highly reduced vegetative habit. Inasmuch as they nest with modern triurids in phylogenetic analyses (Gandolfo et al., 2002), these fossils suggest that the saprophytic habit had evolved within monocots by the Turonian and, given the presumably derived nature of the saprophytic habit in monocots, are indicative of an earlier origin of monocots consistent with timing suggested by minimum age node mapping and some molecular clock-based models (Bremer, 2000). Monocots are not well represented in progressively younger Cretaceous deposits. Zingiberaceae fruits and leaves are found in Campanian deposits, and Musaceae are known from petrified fruits in the Deccan Intertrappean series (Hickey & Peterson, 1978; Friis et al., 2006). Palms appear in the Campanian, and pollen similar to modern grass pollen appears in the Maastrichtian (Crepet et al., 2004; Friis et al., 2006), suggesting that grasses originated earlier than indicated by the first megafossil remains of leaves and florets/pollen in the Lower Eocene (Fig. 7A, B; Crepet & Feldman, 1991). Furthermore, Prasad et al. (2005) have reported fascinating grass and palm remains from the Deccan Intertrappean series, consistent with reports of Cretaceous palm pollen (Harley, 1996; Harley & Zavada, 2000). The monocot fossil record is better in Tertiary deposits, but some major groups have little or no fossil record (e.g., orchids; Daghighian, 1981; Herendeen & Crane, 1995; Gandolfo et al., 2000).

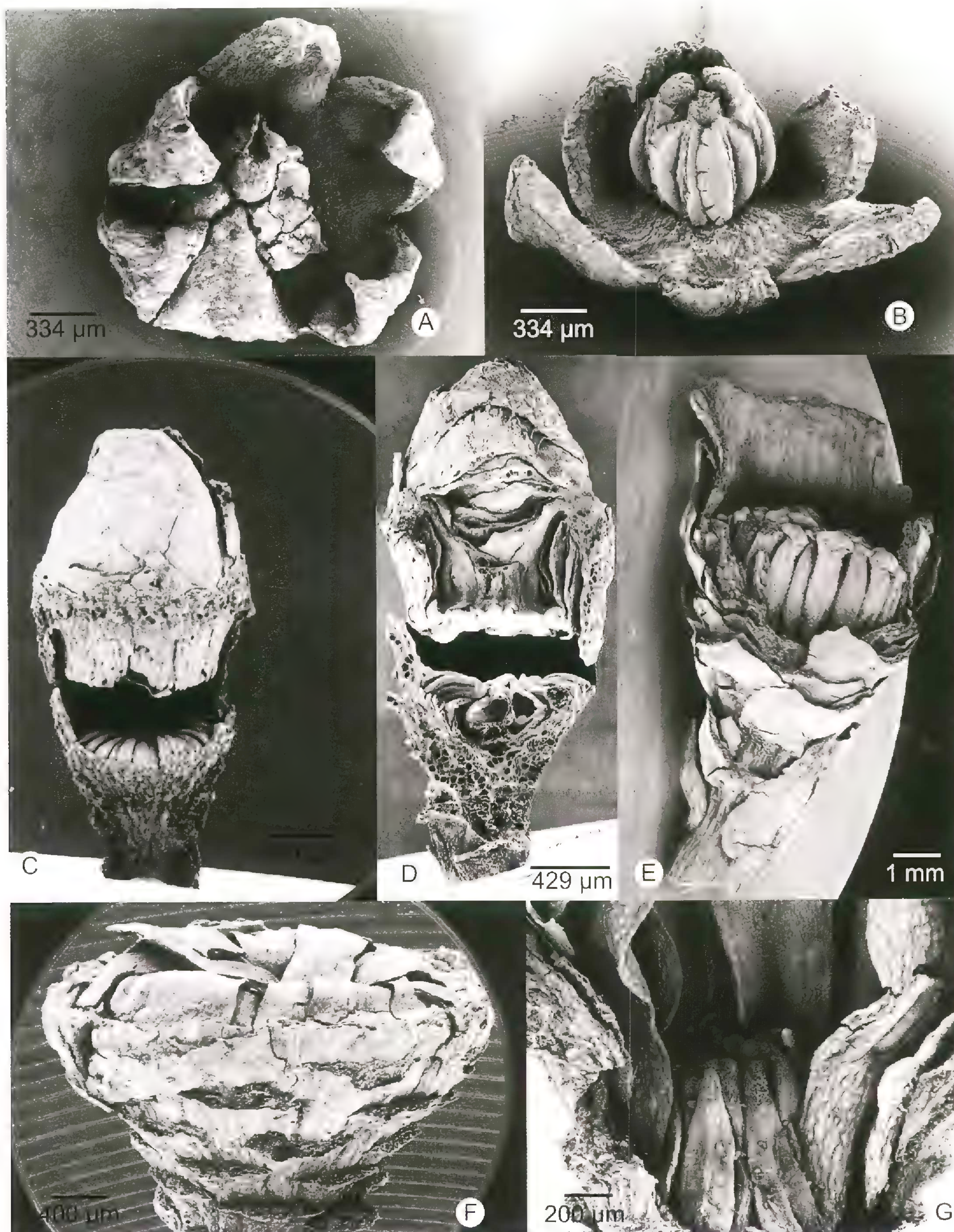


Figure 2. Charcoalfied flowers from the Euronian of New Jersey. —A. Cornell University Paleobotanical collection number CUPC1269. —B. Flowers of Triuridaceae showing six tepals and three stamens with connective extensions (CUPC1260). —C, D. *Microvictoria* (Nymphaeaceae) illustrating the morphology and arrangement of floral parts that conform with those of modern *Victoria* Lindl. in the Nymphaeaceae (CUPC1175). —E. *Cronquistiflora* Crepet & Nixon (Magnoliales) illustrating the tepal-bearing floral cup and numerous spirally arranged carpels (CUPC1175). —F, G. *Detrusandra* Crepet & Nixon (Magnoliales) showing floral cup with incurved stamens and staminodes and spirally arranged carpels within (CUPC1188).

MAGNOLIALES

Fossil flowers of apparent magnolialean affinities are a relatively common component of the Sayreville Turonian angiosperm flora. Interestingly, there are a greater number of magnolialean taxa represented by flower fossils in these sediments than by dispersed pollen (Brenner, unpublished palynological data). This observation raises questions about relative rates of character evolution in Magnoliales, suggesting that pollen character evolution lags floral morphology, a phenomenon also observed in other taxa from these Turonian sediments. Thus, the pollen record by itself may not reveal the full extent of Turonian or earlier magnolialean diversity because dispersed grains representing different taxa may have too many common characteristics to be distinguished. This phenomenon also raises questions about the representative nature of the dispersed angiosperm pollen flora in general in the context of overall patterns of angiosperm evolution.

Among putative magnolialean taxa from Sayreville, two, representing extinct lineages, have been described and have a common characteristic: a cupular receptacle that is also shared by numerous undescribed fossils from the same sediments (Crepet & Nixon, 1998a, unpublished data; Fig. 2E–G). These remain the only two representatives of Magnoliales to be identified in phylogenetic context (Fig. 2E–G) and, while clearly extinct taxa, suggest a minimum age for the Magnoliales of 98 Ma using minimum age node mapping consistent with the compression fossils reported by Crane and Dilcher from Kansas in the U.S.A. However, these have not been verified in phylogenetic context (Dilcher & Crane, 1984; Crane & Dilcher, 1984; Figs. 1C, D, 8B, C). Very interesting new discoveries of entire compressed plants from Brazilian Aptian–Albian deposits have been compared with Magnoliales, but assessments of their affinities have been based on comparisons of characters arranged in tables, a methodology discussed above that suffers from being, essentially, a phenetic approach to identification with inevitable subjective elements (Mohr & Eklund, 2003). The possible weaknesses of this mode of identification are particularly evident in the instance of these Aptian–Albian magnolialean flowers, where comparisons extended to purported affinities with extant Eupomatiaceae are based on the presence of glandular tufts on what are characterized as staminodes in the context of an additional suite of generalized characters. The affinities of these fossils seem in need of further review, given that modern Eupomatiaceae have a distinctive cupular floral receptacle (in contrast to these fossils) and a number of distinctive features that

are either not preserved in these fossils or have not been elucidated by the techniques employed by the authors (Mohr & Eklund, 2003). Thus, the characters that are reported in tables and illustrated there do not seem to convincingly restrict these fossils to the modern taxon Eupomatiaceae.

Generalized Cretaceous angiosperms including these putative Magnoliales are a particularly good example of a critical group of available fossils that should be carefully analyzed in phylogenetic context because it is among this general class of fossils (i.e., Early Cretaceous angiosperms with conduplicate carpels) that valuable insights might be gained into early angiosperm radiation. However, due to their many common features, full understanding of the pattern of evolution of these taxa and its implications is not likely to be gained from uncritical assessments of affinities that do not involve phylogenetic analyses and that tend toward forcing extinct taxa into extant taxonomic categories, thus potentially obscuring information that might otherwise reveal evolutionarily significant patterns. This is an area that needs attention, but the fossil record suggests that the Magnoliales will be older than the conservative estimate provided by Crepet et al. (2004).

CALYCANTHACEAE

The earliest taxon assignable to the Calycanthaceae based on identification in phylogenetic context is *Jerseyanthus* Crepet, Nixon & Gandolfo (Figs. 3A, B, 9A, B; Crepet et al., 2004). This taxon is distinguished by unusual staminodes or “tepals” (Fig. 3A, B; Staedler et al., 2007) and remarkable branched-stamen connective extensions that were discovered in the fossil before reports of less elaborate but similar connective extensions in modern taxa (Staedler et al., 2007). However, there is an earlier report of a fossil member of the Calycanthaceae, *Virginianthus* Friis, Eklund, Pedersen & Crane (Friis et al., 1994), but this fossil taxon is more generalized than modern calycanthoid taxa and, among other things, has monosulcate pollen consistent with a trend in pollen morphology evolutionarily lagging behind floral morphology that has been observed in other taxa discussed in this article. Thus, the presence of more generalized pollen does not necessarily remove this taxon from Calycanthaceae, but, upon phylogenetic analysis including all of its characters, *Virginianthus* appears in an unresolved position basal to the remaining Laurales or as sister to the entire Laurales excluding the Calycanthaceae, while *Jerseyanthus* nests with the monophyletic Calycanthaceae (Crepet et al., 2004).

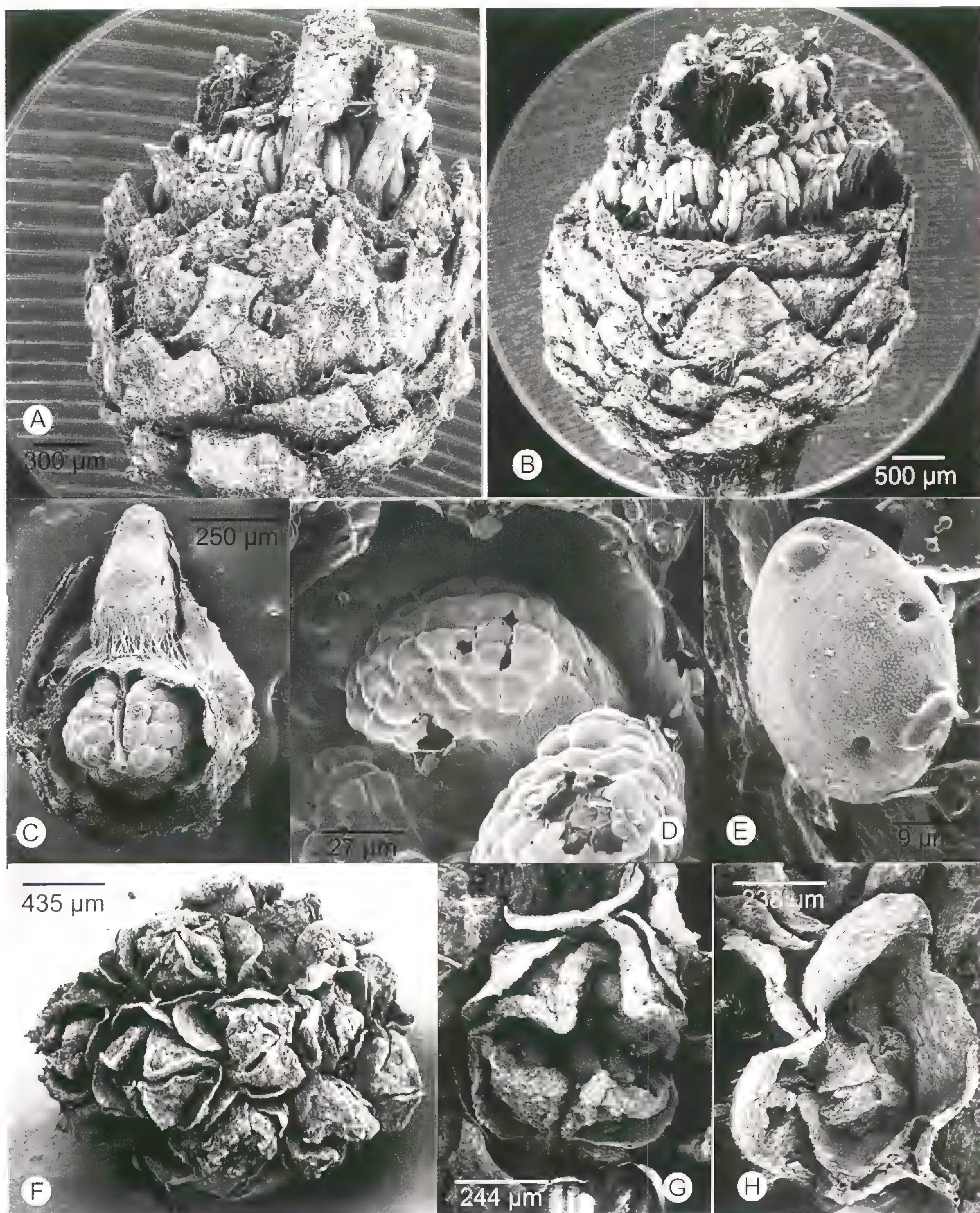


Figure 3. Charcoalfied flowers from the Turonian of New Jersey. —A, B. *Jerseyanthus* (Calycanthaceae) showing stalked staminodes (A) and elaborate connective extensions (B) (CUPC1484). C–E. Flower sharing basic characters with modern Caryophyllales showing well-preserved ovules within the ovary (CUPC1507). —D. A single well-preserved ovule showing its campylotropous nature. —E. A pantoporate pollen grain from one of the anthers. F–H. A hamamelidaceous staminate inflorescence showing stamens within a tepal cup (F, G). —H. A floret with stamens removed to illustrate the position of the staminodes (CUPC1160).

CARYOPHYLLALES

The Caryophyllales have only been reported once from Cretaceous deposits (Nixon & Crepet, 1993b). These Turonian fossil flowers may represent this order

based on very distinctive pantoporate pollen and generally similar floral morphology (Figs. 3C–E, 9C, D), but there are differences, notably partitions retained in the ovary, but these could be the result of the fossils having been preserved at a relatively early

developmental stage, consistent with the early developmental stages of the well-preserved campylotropous ovules (Fig. 3D; Nixon & Crepet, 1993b). Although they possess significant synapomorphies that define the caryophylls, these fossils have not been fully analyzed in phylogenetic context and these results are preliminary.

CORE EUDICOTS, SAXIFRAGALES, HAMAMELIDACEAE

Exceptionally preserved staminate and pistillate inflorescences and detached stamens have been discovered from Turonian deposits at the Crossman site in New Jersey, U.S.A. (ca. 88.5–90.4 Ma) in the Raritan Formation of New Jersey (Crepet et al., 1992; Fig. 3F–H). The fossils have a combination of floral and pollen characters found in various genera of modern entomophilous and anemophilous Hamamelidaceae and anemophilous *Platanus* L. (Platanaceae), including a sepal cup, staminal tube, and apparently nectariferous staminodes (these characters are consistent with insect pollination). This unnamed fossil taxon (Fig. 3F–H), while grouping with modern Hamamelidaceae in phylogenetic analysis, is an example of a mosaic of familial-level characters relative to modern taxa and might have been hard to place outside of phylogenetic context (i.e., the character table comparison method would result in subjective assignment). Interestingly, these fossils have apparent staminodal nectaries (based on position and structure) with morphology intermediate between the fossils' functional stamens and modern hamamelidaceous petals (Fig. 3H). They are positioned within the fossil flowers where petals are found in modern related genera (Fig. 3H), suggesting the possibility that petals originated from such staminodes in the hamamelid lineage. The appearance of the character complex embodied in these flowers during the late Middle Cretaceous may signal the early stages of the relationship between specialized pollinators, such as bees, and the hamamelid–rosid–asterid lineage of angiosperms, arguably one of the most important events in angiosperm radiation (Crepet et al., 1991; Crepet, 1996) and one reflected in the contemporary record of other angiosperms (Figs. 12, 13).

CORE EUDICOTS, SAXIFRAGALES, ALTINGIACEAE

Zhou et al. (2001) described fossil capitate inflorescences that have perigynous florets with a hypanthium, two-carpellate gynoecea, unisexual flowers, phyllomes, numerous ovules per carpel, a three-layered carpel wall, and tricolpate reticulate pollen (Fig. 4A, B). Vessels in the inflorescence pedicel have scalariform perforation plates with oblique end

walls and scalariform and opposite/alternate intervacular pitting (Zhou et al., 2001). As in the case of the fossil hamamelidaceous inflorescences described above, this fossil taxon includes a mixture of characters relative to the sets found in modern taxa within Hamamelidaceae, but cladistic analysis suggests that these fossils represent a basal member of the Altingiaceae that lacks the derived pollen found in extant Altingiaceae and retains the more plesiomorphic tricolpate pollen found in most of the Hamamelidaceae. This phenomenon, i.e., generalized pollen relative to morphology of the flower and inflorescences, is observed in other fossil angiosperm taxa from these Turonian sediments (including the Iteaceae; Hermsen et al., 2003). Also, as in the case of the hamamelidaceous taxon above, certain characters of the fossil including phyllomes with stomata, short and straight styles, and small perprolate pollen grains also indicate the possibility of insect pollination.

CORE EUDICOTS, SAXIFRAGALES, ITEACEAE

Fusainized three-dimensionally preserved flowers from the Turonian Raritan Formation of New Jersey (*Divisestylus brevistamineus* Hermsen, Gandolfo, Nixon & Crepet and *D. longistamineus* Hermsen, Gandolfo, Nixon & Crepet) provide another example of fossil taxa whose character complements are not found in any single extant family (Figs. 4C–E, 10C, D). In cases of this nature, tabular comparisons might lead to subjective assignments of affinities through some sort of intuitive character weighting, whereas inclusion of their characters in phylogenetic analysis provides an objective and transparent method for assessing their relationships. These are the kinds of analyses that also reveal trends in character evolution within monophyletic groups. These fossil species (*D. brevistamineus* and *D. longistamineus*) share characters with both Saxifragaceae and Iteaceae in the order Saxifragales. Similarities include a pentamerous perianth, calyx fused below into a hypanthium with free sepal lobes above, haplostemonous androecium with stamens situated opposite the calyx lobes, inferior ovary, bicarpellate gynoeceum, numerous ovules on axile placentas, conspicuous intrastaminal nectary ring, and capsulate fruits that open apically. Distinctively, carpels and stigmas are fused, while the styles are free, indicating closer affinities with extant Iteaceae, whereas other characters, such as basifixed anthers in *D. brevistamineus*, tricolpate and striate pollen grains, and anomocytic stomata, indicate closer affinities to Saxifragaceae. Cladistic analyses using molecular and morphological characters, and morphological characters only (Hermsen et al., 2003), however, demonstrate that these

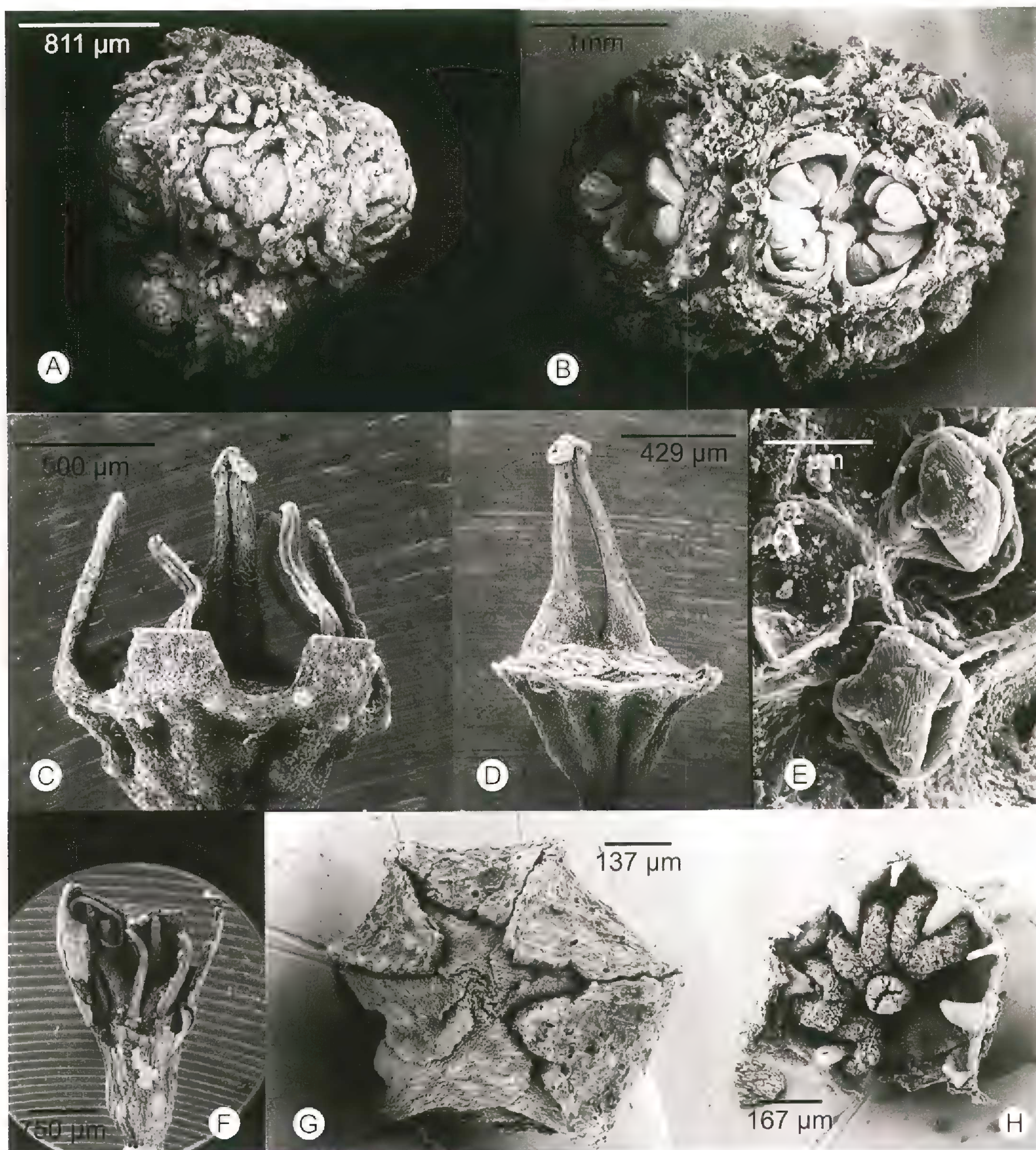


Figure 4. Charcoalified flowers from the Turonian of New Jersey. —A–B. *Microaltingia* Zhou, Crepet & Nixon (Altingiaceae) with bicarpellate florets, phyllomes, and numerous ovules/carpel (A, CUPC1064; B, CUPC1063). C–E. *Divisestylus longistaminus* (Iteaceae). Elongate distally fused styles are distinctive characters of this taxon. —C. Sepals and elongate stamens (CUPC1349). —D. Fusion at the stigmas (CUPC1359). —E. Tricolporate pollen on an anther (CUPC1359). —F. Myrtalean flower with an elongate floral tube, two incurved styles, and coiled stamen filaments (CUPC1510). —G, H. Myrtaceae, hexamerous flower with contorted corolla lobes, phyllomes alternating with stamens, and hexamerous, epigynous ovary (CUPC1506).

fossils share a more recent common ancestor with Iteaceae than Saxifragaceae, thereby making *Divisestylus* Hermsen, Gandolfo, Nixon & Crepet the oldest fossil taxon known with clear affinities to Iteaceae. These fossil taxa are distinguished by having tricolporate pollen (Fig. 4E), a more generalized pollen apertural configuration than the dicolporate pollen found in modern species of Iteaceae.

ROSIDS, MYRTALES

Myrtaceae are not definitively represented by fossil evidence until approximately 65 Ma (Crepet et al., 2004); however, Turonian fossils with a hypanthium, elongate floral tubes, and coiled stamen filaments may be examples of the Myrtaceae (Fig. 4F). These fossils require further study and, despite their apparent

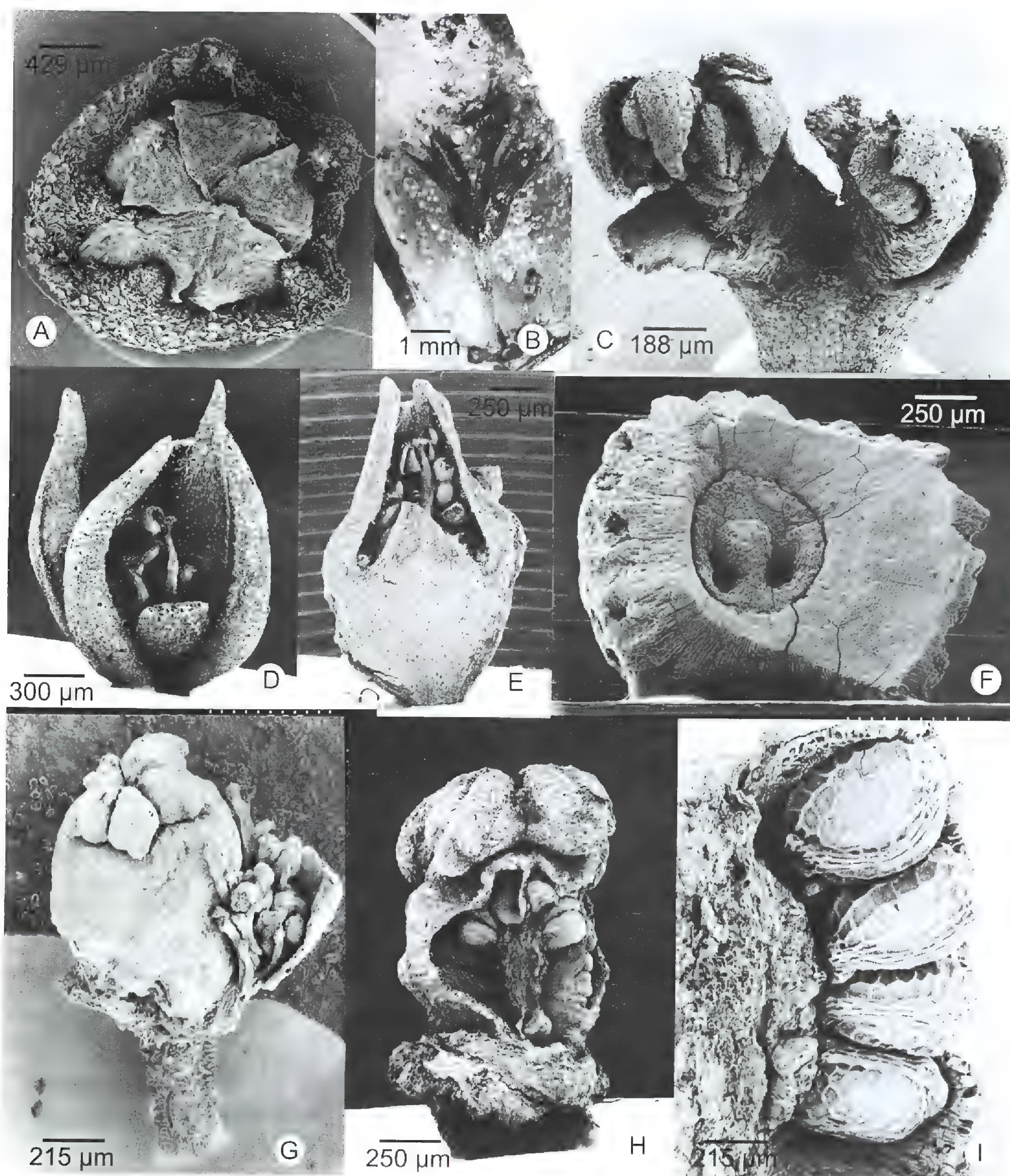


Figure 5. —A. *Astronia cumingiana* (BH79113) in modern Myrtaceae. —B. Fossil fagalean inflorescence preserved in amber from the Turonian of New Jersey. C–I. Charcoalified flowers from the Turonian of New Jersey. —C. Part of a robust inflorescence bearing bisexual fagalean florets similar to those illustrated as seen in Fig. 5E. —D. Staminate fagalean floret. —E. Bisexual fagalean floret. —F. Fruit of Juglandaceae. G–I. *Paleoclusia*. —G. Flower with cuneiform stigmas and fascicled stamens. —H. Pistil with broken ovary wall revealing anatropous ovules. —I. Mature seeds within the ovary.

possession of certain synapomorphies, phylogenetic placement to confirm apparent affinities.

Well-preserved flowers having a set of characters typical of less-specialized Melastomataceae (e.g., as in *Astronium* Jacq.; Fig. 5A) are also found in Turonian deposits (Figs. 4G, H, 5A, 10E, F). These fossils, if their affinities are con-

firmed, may resolve disputes about a possible Gondwanan origin of melastomes by revealing that they originated early enough so that complex long-distance dispersal models are not needed to explain their modern-day distribution (Raven & Axelrod, 1974; Renner et al., 2001; Morley & Dick, 2003).

EUROSIDS I. FAGALES

Flowers, inflorescences, and pollen (Figs. 5C–E, 11A, B) and another taxon represented by flowers in amber (Fig. 5B) suggest Fagales were extant by the Turonian (Nixon & Crepet, 1994). Charcoalified mesofossils have six tepals in two whorls and are either staminate (Figs. 5D, 11A, B), or bisexual with a well-developed ovary (Figs. 5E, 11B). They are linked by similar floral structure and identical pollen. There are six stamens in each type of flower, and in staminate florets, stamens consist of long filaments and dorsifixed anthers bearing tricolporate pollen with exine micromorphology similar to that of modern castaneoids and generalized Saxifragales. Stamen filaments are flanked by globose structures bearing trichomes that may be part of a nectary disc or represent separate nectaries (Fig. 11A). Ovaries are tricarpellate trigonous and slightly winged as in fruits of certain modern Fagaceae (Figs. 5E, 11B). There are three recurved styles with adaxial grooves (Fig. 11B). Characters of flowers in conjunction with compact, apparently fleshy bisexual flower-bearing inflorescences (Fig. 5C) suggest a morphocline leading to the more compact inflorescences observed in more recent Fagales (Nixon & Crepet, 1994; Sims et al., 1998) and, ultimately, to cupules characteristic of modern Fagales and are indicative of fagalean affinities that have been preliminarily confirmed by phylogenetic analyses (Gandolfo et al., in prep.). The floral characters also suggest insect pollination because the combination of well-developed tepals, nectaries, and pollen of a size incompatible with wind dispersal (Whitehead, 1969) is indicative of insect pollination. Insect pollination in ancestral Fagales would also be compatible with apparent insect pollination in early Platanaceae as suggested by Friis et al. (1988) and also with floral characters in early Juglandales that also are consistent with insect pollination, suggesting that extant wind-pollinated hamamelids are derived with respect to pollination biology.

EUROSIDS I. JUGLANDALES

Excellent preserved fossils of Juglandales from Santonian Coniacan deposits have provided the first important insights into the affinities of the *Normapolles*-bearing taxa and the history of the Juglandales (e.g., Friis, 1983; Sims et al., 1999; Schönenberger et al., 2001) and have provided further insights into pollination biology of early Juglandales. Several inflorescence fragments with associated *Normapolles* pollen and nuts (Nixon, in prep.; Fig. 5F) suggest Juglandales were present by the Turonian.

EUROSIDS I. MALPIGHIALES, CLUSIACEAE

Remarkably well-preserved flowers are five-merous with fascicled stamens and cuneiform stigmas and are almost identical to flowers of modern Clusiaceae in every respect down to pollen morphology and resin canals in the floral tissues (Fig. 5G–I). These flowers group with modern Clusiaceae in phylogenetic analysis (Crepet & Nixon, 1998b).

EUROSIDS II. BRASSICALES (CAPPARALES)

A distinctive Turonian taxon is represented by flowers having a combination of characters now found in families in the order Capparales (now included in Brassicales; Angiosperm Phylogeny Group, 2003). This taxon, *Dressiantha* Gandolfo, Nixon & Crepet (Gandolfo et al., 1998b), has flowers with a well-developed gynophore, a distinctive sepal arrangement, an unequal petal size (bilaterality), monothecal anthers, and a bicarpellate gynoecium, characters found in extant families in the order Brassicales (Angiosperm Phylogeny Group, 2003; Fig. 6D–F). This taxon represents the oldest known fossil record for the Brassicales and has been important in dating in the history of the related extant taxon *Arabidopsis* (DC.) Heynh. Interestingly, in a recent paper, de Craene and Haston (2006) place the fossil in a different morphology matrix from the one used by Gandolfo et al. (1998b), who used the Rodman (1991a, b) matrix. The de Craene and Haston matrix was larger and included characters, such as wood anatomical features, not found in the *Dressiantha* fossil. It may be that the resultant addition of missing values for *Dressiantha* in their matrix might account for the anomalous change in the position of this fossil taxon from Brassicales to Sapindales. The change is anomalous because, as discussed by de Craene and Haston (2006), there is no conflict between morphological characters found in Brassicales and those displayed by the fossil flowers. This is a good example of the value of the medium of phylogenetic context in discussing affinities of fossil taxa. Different outcomes can be objectively analyzed and explained; new questions can be posed in a level of discourse that is both appropriate and potentially illuminating.

ASTERIDS, ERICALES OR ERICANAE, THEACEAE

Flowers five-merous with three carpels, fascicled stamens, and tricolporate pollen represent Theales, are diverse in the Turonian deposits of northern New Jersey (Figs. 6A, 11C, D; Crepet et al., 1996), and are also represented in somewhat younger (Campanian) deposits in Georgia (Keller et al., 1996).

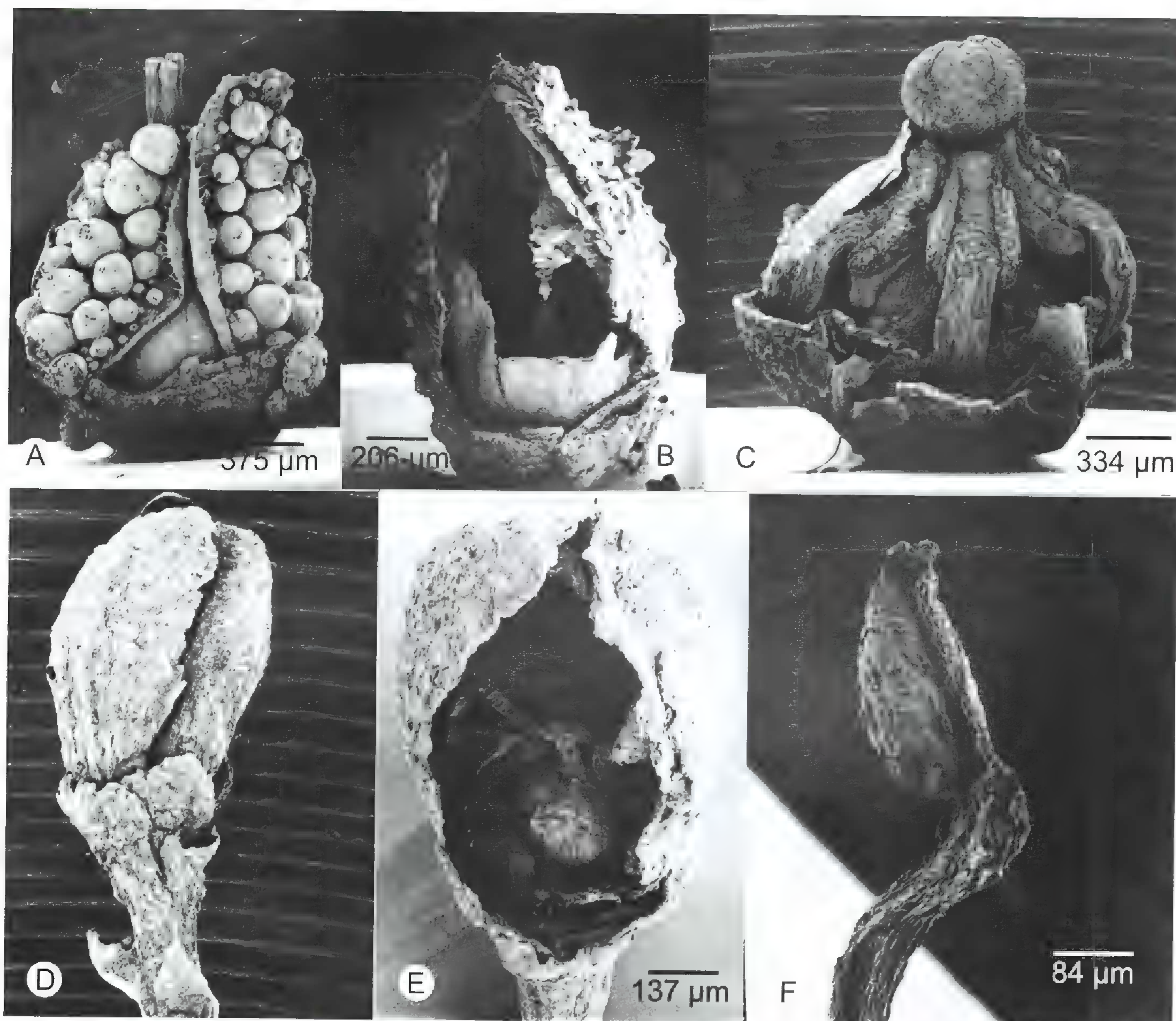


Figure 6. Charcoalified flowers from the Turonian of New Jersey. —A. A Thealean flower with remarkable abaxial sepal glands. —B. *Paleoenkianthus* Nixon & Crepet (Ericaceae) flower bud broken to show the corolla, pistil, and stamens within. —C. An ericalean flower with stamen tubules. D–F. *Dressiantha* (Brassicales). —D. Flower illustrating the bilaterally symmetrical corolla in bud. —E. An open flower bud showing the pistil and parts of stamens. —F. A single stamen illustrating the geniculate filament.

ASTERIDS, ERICALES OR ERICANAE, ERICACEAE

Fossils of Ericanae are interesting and appear first in Turonian deposits (Figs. 6B, C, 11E, F) and shortly thereafter in Santonian–Campanian deposits of Sweden (Friis, 1985; Schönenberger & Friis, 2001). They are remarkably diverse in the Turonian and demonstrate a complex of characters that is now associated with highly specific, usually apid pollinators. Among these, a more general and basal Ericalean taxon has elongate sepals, nectary disc, carpels with separate stigmas, a sympetalous corolla, and two whorls of stamens with stamen awns (Nixon & Crepet, 1993a). A more interesting association of closely related, more derived ericalean taxa is linked by a basic five-merous floral plan and a set of shared but variable characters (Figs. 6C, 11E, F). These include abaxial sepal glands, sepal

indumentum, haplostemony, dorsifixed anthers, basic pollen morphology, flattened stamen filaments, staminodal nectaries, and superior ovaries with five-lobed stigmas having distinctive circular indentations at the junctures of the lobes. However, there are distinct variants representing at least three taxa and probably more. One taxon has anthers without appendages or tubules, elongate stamen filaments, monadinous pollen grains, a non-globose stigma, and fruits that are loculicidal capsules. This taxon is the best known among this complex because flowers are occasionally preserved in inflorescences (Fig. 11E). Flowers are subtended by two bracteoles in the axil of foliar bracts (Fig. 11E). Leaves associated with these fossils are folded, with marginal glands similar to those found on the margins of the sepals of flowers representing this taxon (Fig. 11E, F).

A second taxon differs from the first ericad of this five-merous complex in having differently distributed sepal glands, shorter stamen filaments (anthers do not extend beyond the stigma height), stamen filaments with distinctive stellate trichomes that are also found on the pistil, anthers that are notched and have tubules (Fig. 6C), and pollen that is apparently in loose polyads connected by short viscin threads. Both fossil taxa group within Ericaceae upon phylogenetic analysis (Crepet et al., 2004).

OVERVIEW OF THE ANGIOSPERM FOSSIL RECORD IN THE APTIAN–TURONIAN INTERVAL

There is a striking pattern in the fossil records of both angiosperm taxa and their defining floral characters within this interval that has a number of interesting and possibly meaningful implications. Early Cretaceous taxa have a relatively sparse but significant record that has already revealed the timing of the occurrences of major events in angiosperm history including the possible origin of the angiosperms, the evolutionary assembly of the bisexual flower, the origin of the floral envelope, and the origins of several major angiosperm lineages, including the eudicots, accompanied by a corresponding diversification of pollen types. In addition, Early Cretaceous angiosperm fossils include representatives of what appear to be extinct taxa basal to existing lineages such as Nymphaeaceae. Existing evidence indicates that Early Cretaceous taxa included the ANITA clade + Chloranthaceae + the early tricolpate lineages: platanoids and Buxaceae (Drinnan et al., 1991; Pedersen et al., 1991, 1994; Friis et al., 2006). The modern-day diversity of taxa that first appear in the Early Cretaceous is relatively low, with little indication from known fossils that they might have once been more speciose (Magallón et al., 1999; Crepet et al., 2004; Friis et al., 2006). With respect to function, fossil flowers of this time were either structurally appropriate for coleopteran pollinators or suggestive of generalized kinds of insect pollination that may have involved Coleoptera, Diptera, early Lepidoptera (Micropterigidae), and, conceivably, even hymenopteran lineages transitional to Apidae (Thein, 1980; Grimaldi, 1999; Grimaldi & Engel, 2005). The uniformly small floral fossils of this age suggest that their pollinators at least included very small insects (Friis et al., 2006). The possibility that some of these taxa may have been wind pollinated has been raised by Dilcher (2000).

The lower Late Cretaceous time frame (more or less the middle of the Cretaceous), including the Cenomanian, Turonian, and Coniacian ages, is important because angiosperms became dominant in species

numbers (inferred from modern-day diversity in clades that appear by that time) during this interval (Fig. 12) and because there was a dramatic coincidence of co-occurring factors that may be significant in explaining some measure of the success of the flowering plants. These include: (1) The striking peak in diversity of angiosperm taxa. There are ca. 39,000 species today included in the dicot taxa known to have existed by that time. Although the early record of the monocots is too fragmentary to give an accurate idea of actual monocot diversity during this Middle Cretaceous interval, they were almost certainly present in greater numbers than indicated by the known fossil floral record, and, thus, total angiosperm species diversity was likely to have been even greater than reliable evidence now indicates. (2) The earliest (Cenomanian) appearance of the first cyclic eudicot flower that had both petals and sepals in addition to definite numbers of floral parts (Figs. 1E, F, 8D; Basinger & Dilcher, 1984). Also note that cyclic floral parts in other configurations are considered widespread if not fundamental to most angiosperm taxa by some authors (e.g., Zanis et al., 2003). (3) The dramatic Turonian appearances of a wide variety of floral morphologies, some now specifically associated with more derived pollinators including hymenopterans (Fig. 13). The evolution of some of the latter floral types (e.g., those having a fused corolla or bilateral symmetry, etc.) would logically have depended on the prior occurrence of the relatively simple cyclic flower because these more specialized configurations would not have been attainable in a single step from ancestors with a more generalized floral plan that included at least some multiple spirally arranged floral parts (Endress, 2001). Given the timing observed in the fossil record (i.e., the rapid appearance of derived floral configurations closely following the appearance of the cyclic flower with regular numbers of parts), various floral specializations for more derived pollinators must have evolved rapidly in the Cenomanian–Turonian interval, indicating possibly rapid adaptation to radiating hymenopteran or other highly derived pollinators. This possibility is consistent with the first appearances in the Turonian of taxa that are now specifically and closely associated with particular and derived Apidae (e.g., the Clusiaceae, *Paleoclusia* Crepet & Nixon, with Meliponini). In addition, this fossil Clusiaceae indicates that even at this relatively early stage of their history, at least some of these fossil taxa apparently had the same reward structure as their modern relatives (in this instance, resins; Crepet & Nixon, 1998b). (4) Timing of the early fossil record of bees. The observed Middle Cretaceous burst of angiosperm species diversity is followed relatively closely by the first fossil evidence

of bees. The earliest bees are preserved in Upper Albian Burmese amber (Poinar & Danforth, 2006), and another fossil bee that shares many characters with modern Meliponinae is preserved in apparently Upper Cretaceous amber of uncertain age (Grimaldi, 1999; Engel, 2000), but the possibility that this fossil from New Jersey is of Turonian or even earlier in age is supported by the presence of the fossil *Paleoclusia* noted above from Turonian deposits of New Jersey, U.S.A., with similar morphology and the same apparent reward system that today ties the Meliponinae to the Clusiaceae (Crepet & Nixon, 1998b).

POST-TURONIAN CRETACEOUS DEPOSITS

The post-Turonian pre-Maastrichtian fossil record of angiosperms is not as complete as that of the record in the Cenomanian–Turonian interval and, so far, has failed to provide a corresponding level of detail of subsequent Late Cretaceous angiosperm radiation. As it is presently understood, the fossil record documents a limited (but significant) number of innovations between the Turonian and Maastrichtian. This interval is characterized by the radiation of rosoid orders Fagales and Juglandales that appear first in the Turonian, represented by flowers, partial inflorescences, and fruits (Fig. 5F; Sims et al., 1998). Inferences from other carefully analyzed plant organs, while perhaps risky without more detailed knowledge of the relative rates of evolution among different plant organs, do suggest that monocot diversification proceeded throughout the Upper Cretaceous with evidence of Zingiberales (fruits and leaves) and palms (fruits, pollen, and leaves) in this interval (Hickey & Peterson, 1978; Daghljan, 1981; Herendeen & Crane, 1995; Gandolfo et al., 2000). Maastrichtian floral remains are generally not preserved in great detail but are significant because the record of monocots suggests that they had radiated considerably by this time, consistent with the occurrence of Triuridaceae in the Turonian and other Lower Cretaceous remains that have been attributed to monocots. Finally, as noted above, pollen with morphological and structural features compatible with the distinctive pollen of grasses is known from Maastrichtian deposits (Linder, 1986; Crepet & Feldman, 1991), and grass-like leaf remains have been isolated from Maastrichtian dinosaur coprolites (Prasad et al., 2005), further suggesting that monocots had radiated relatively invisibly during much of the Cretaceous. Interestingly, there is not a great deal of evidence in the pre-Maastrichtian–Late Cretaceous of taxa with the kinds of fruits that are adapted for animal seed dispersal in groups that now are characterized by such dispersal mechanisms (e.g., some Juglandaceae and Fagales).

EARLY TERTIARY–PALEOGENE

There is a burst in Tertiary angiosperm diversification characterized by the radiation of grasses, radiation of Fagaceae and Juglandaceae, appearance and radiation of Euphorbiaceae (Crepet & Daghljan, 1982, unpublished data), legumes (mimosoid, caesalpiniod, and papilionoid, Fig. 7C–E; Herendeen & Crane, 1992; Lavin et al., 2005), and many asterids in the Asterid I clade (although the fossil record of reliably identified asterids is relatively sparse; Crepet et al., 2004; Friis et al., 2006). This interval represents a period of modernization for many taxa and is also characterized by the radiation of many pollinating insects including the Macrolepidoptera. The Tertiary record of bees is relatively good (Grimaldi, 1999; Grimaldi & Engel, 2005). Perhaps the most dramatic innovations in the Tertiary include the brush flower/inflorescence (mimosoid legumes), the papilionoid legume flower with its pronounced zygomorphy, and the prolonged corolla tube (Fig. 7C–F). In addition, the Tertiary is characterized by the radiation of additional taxa (e.g., asterids and grasses), which include modern relatives with herbaceous habits.

DISCUSSION

There are a number of central questions surrounding angiosperm history in the context of updated fossil evidence.

ANGIOSPERM ORIGIN AND EARLY RADIATION

Additional clarification of the structures of early fossil angiosperms and analysis of their relationships in phylogenetic context promise to illuminate early angiosperm history and perhaps to reveal certain important homologies, and already pose certain questions. For example, were early angiosperms apetalous? Are sepals *de novo* organs, are they modified stamens, or do they have multiple origins and homologues? Did the flower originate by coalescence of reproductive structures borne on elongate axes such as those of *Archaeofructus*, and do a number of Early Cretaceous angiosperm flowers represent a morphocline linking *Archaeofructus*-like ancestors with condensed flowers, or is this model too simplistic and not supported in phylogenetic context? Such clarifications, if forthcoming and if conducted within a phylogenetic framework, may complement genetic studies of MADS-box genes and transcription factors known to influence floral development in ways that might reveal homologies between angiosperm reproductive structures and those of non-angiosperms (e.g., Theissen et al., 2000).



Figure 7. Tertiary compression fossils from the Paleocene–Eocene of Tennessee, U.S.A. —A. Grass spikelet with two florets. —B. Grass rhizome with leaf sheaths. —C. *Protomimosoidea* Crepet & Taylor flower with developing legume. —D. *Protomimosoidea* flower. —E. *Barnabyanthus* Crepet & Herendeen, the earliest papilionoid flower in the fossil record. —F. A flower (Asterid I?) illustrating that the funnelform corolla is well developed at this time.

ANGIOSPERM DOMINANCE IN SPECIES NUMBERS

Given the scale of angiosperm preeminence in modern plant species diversity and its obvious ecological significance, the matter of angiosperm predominance and success has received a great deal of attention and continues to be an area of considerable interest, speculation, and controversy (Raven, 1977; Regal, 1977; Doyle, 1978; Burger, 1981; Stebbins, 1981; Niklas et al., 1983; Crepet, 1984, 1996; Tiffney, 1984, 1986; Eriksson & Bremer, 1992; Waser, 1998; Grimaldi, 1999; Magallón et al., 1999; Verdú, 2002; Feild et al., 2004; Fenster et al., 2004; Grimaldi & Engel, 2005; Friis et al., 2006). There is little doubt that there are separate and possibly complementary reasons for the present level of angiosperm species diversity (Raven, 1977; Crepet, 1984; Tiffney, 1984; Eriksson & Bremer, 1992; Tiffney & Mazer, 1995; Verdú, 2002; Fenster et al., 2004). There have been appraisals of the correlations

between diverse angiosperm taxa and derived pollinators (including vertebrates; Raven, 1977), assessments of the potential significance of animal seed dispersers (Tiffney, 1984), and examinations of the possible effects of synergy among multiple factors (e.g., Raven, 1977; Regal, 1977; Crepet, 1984; Tiffney, 1984; Eriksson & Bremer, 1992). In addition, consideration has been given to factors involved in minimizing extinction, as well as to those involved in promoting speciation (Tiffney & Mazer, 1995). There have been challenges to various hypotheses linking angiosperm success to various factors including pollinator specificity and efficiency following the model first proposed by Verne Grant (1949; e.g., Midgely & Bond, 1991; Waser, 1998; Fenster et al., 2004). While there are obvious correlations between hyperdiverse taxa and insect pollinators (e.g., orchids and euglossine bees; Dressler, 1968, 1982), there are obvious alternative attributes or circumstances that may have been responsible for high species diversity

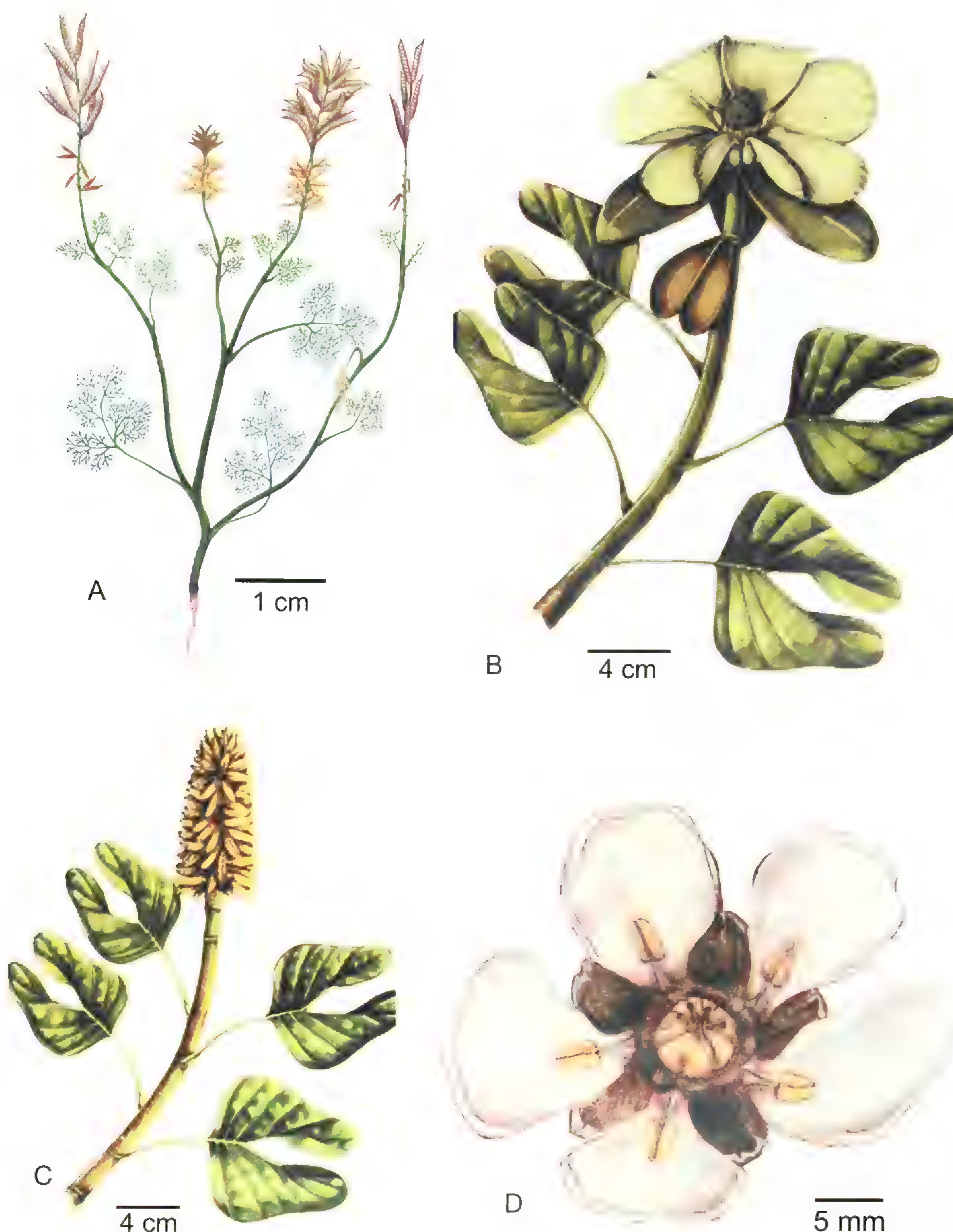


Figure 8. Reconstructions with permission of D. L. Dilcher, Florida Natural History Museum. —A. *Archaeofructus*. —B. *Archaeanthus* flower. —C. *Archaeanthus* fruit. —D. Eudicot flower from Rose Creek.

within particular monophyletic groups. Sorting out the relative influences remains very much at issue, and, as molecular genetics studies continue to reveal more about genetic control mechanisms and within-species reproductive barriers (hybrid necrosis; Bomblies & Weigel, 2007), we might reasonably expect the discovery that other factors have had important roles in promoting species diversification in angiosperms.

Currently, our understanding of the fossil record of angiosperms is much improved and more reli-

able, and we have a better idea of the pattern of appearances of angiosperm families, floral characters, and possible insect pollinators. Likewise, we have this knowledge in the context of a more accurate understanding of overall angiosperm relationships (Soltis et al., 2000), such that some questions concerning angiosperm success can be addressed from a fresh perspective. However, in considering the phenomenon of angiosperm diversification through geologic time, it is important to frame the major ques-

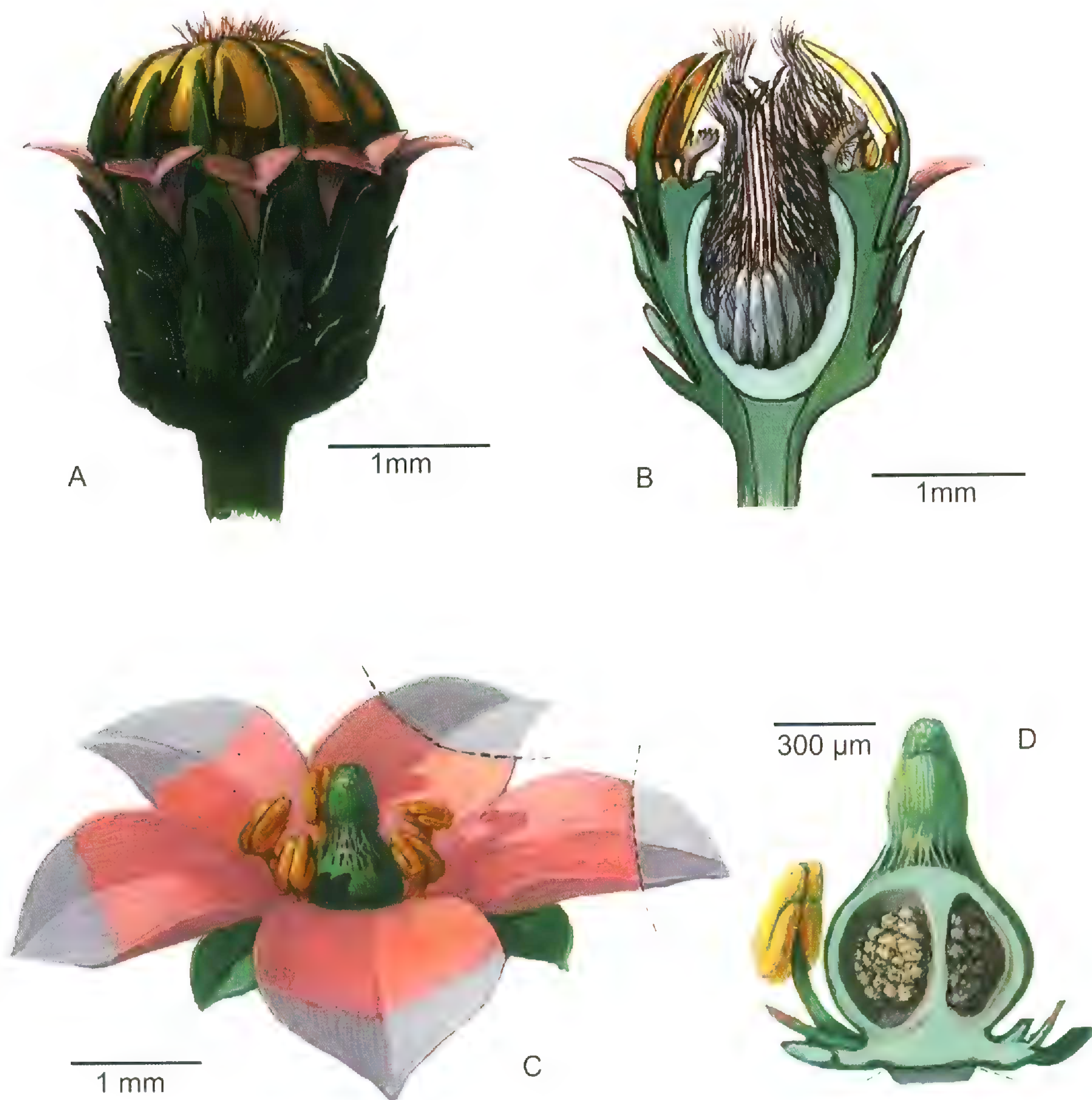


Figure 9. Reconstructions of Turonian fossil flowers with permission of Michael Rothman. —A, B. *Jerseyanthus* (Calycanthaceae). —C, D. ?Caryophyllales.

tions before proceeding to examine how recent, more complete, and reliable evidence affects our possible understanding of them.

With respect to timing, one can ask two questions about angiosperm preeminence in species numbers: (1) When do angiosperms become dominant in species number (measured by first appearances of modern diverse groups), and what are the circumstances that might have been relevant based on timing? (2) How did even greater angiosperm diversity arise following the initial attainment of angiosperm dominance in numbers of plant species?

It is interesting to examine fossil evidence now available with respect to the questions above and to consider whether it rules out any possibilities, such as insect involvement in preeminent angiosperm diversity, due to timing considerations. As noted in the

preceding summary of the angiosperm fossil record, conservative estimates of timing in first appearances of angiosperm families suggest that the angiosperms had become dominant by the Turonian (ca. 90 Ma). In fact, families appearing by Turonian times now encompass approximately 39,000 species (Fig. 12), while all gymnosperm and vascular non-seed plant taxa combined today only include about 22,000 species. The dramatic coincidence of characters associated with advanced modes of insect pollination by the Turonian (Fig. 13), the similarity of certain Turonian angiosperm taxa to those now specifically associated with such pollinators, and the proximally temporal fossil evidence of the earliest bees are consistent with insect involvement in the Cenomanian–Turonian proliferation of angiosperm species according to mechanisms discussed by Grant (1949).

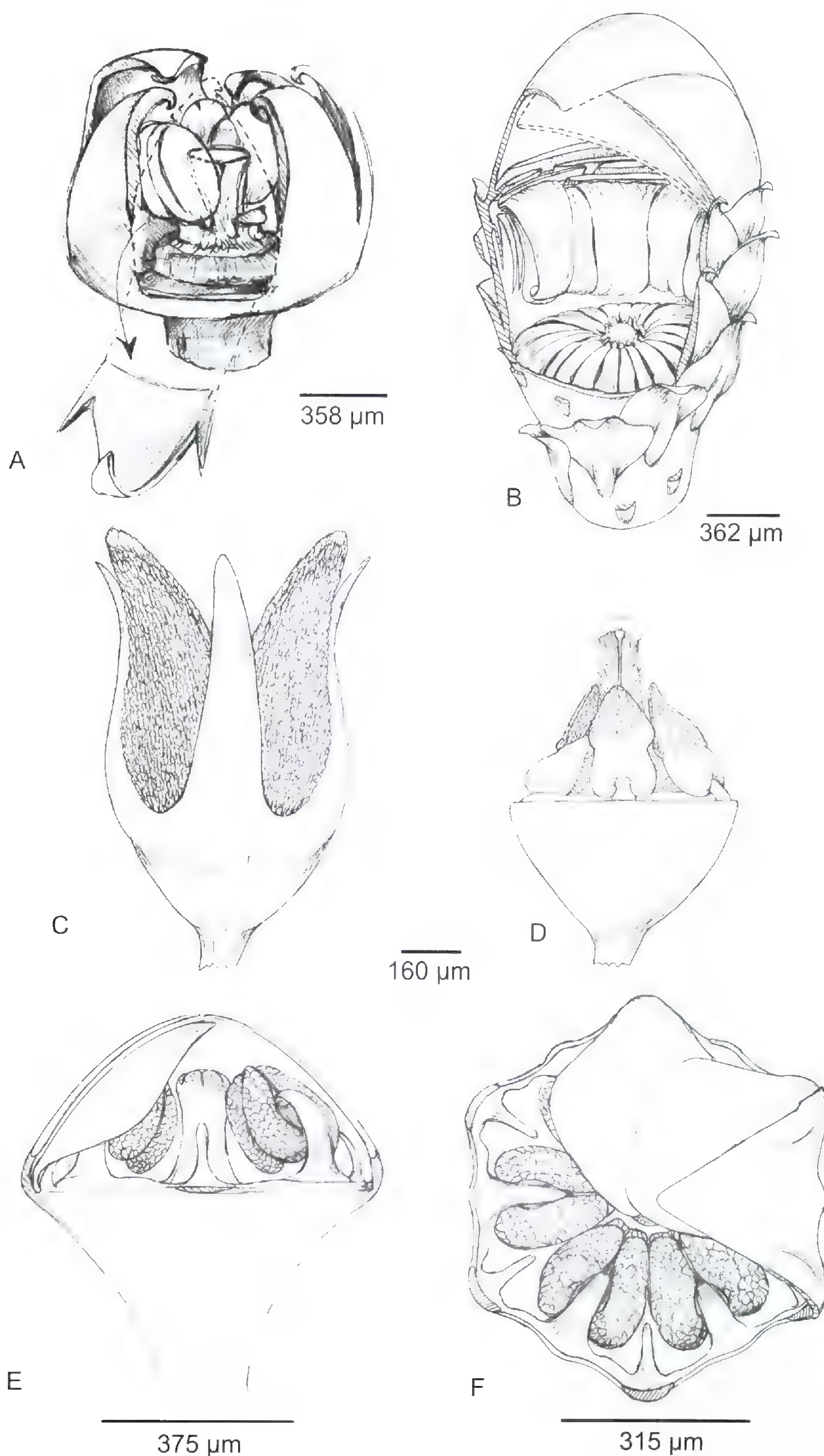


Figure 10. Reconstructions of Turonian fossil flowers with permission of Michael Rothman. —A. *Mabelia* (Triuridaceae) illustrating a fossil species with a staminal column, a character also found in modern Triuridaceae. —B. *Microvictoria*. —C. *Divisestylus longistamineus*. —D. *Divisestylus brevistamineus*. —E, F. Reconstructed fossil Melastomataceae.

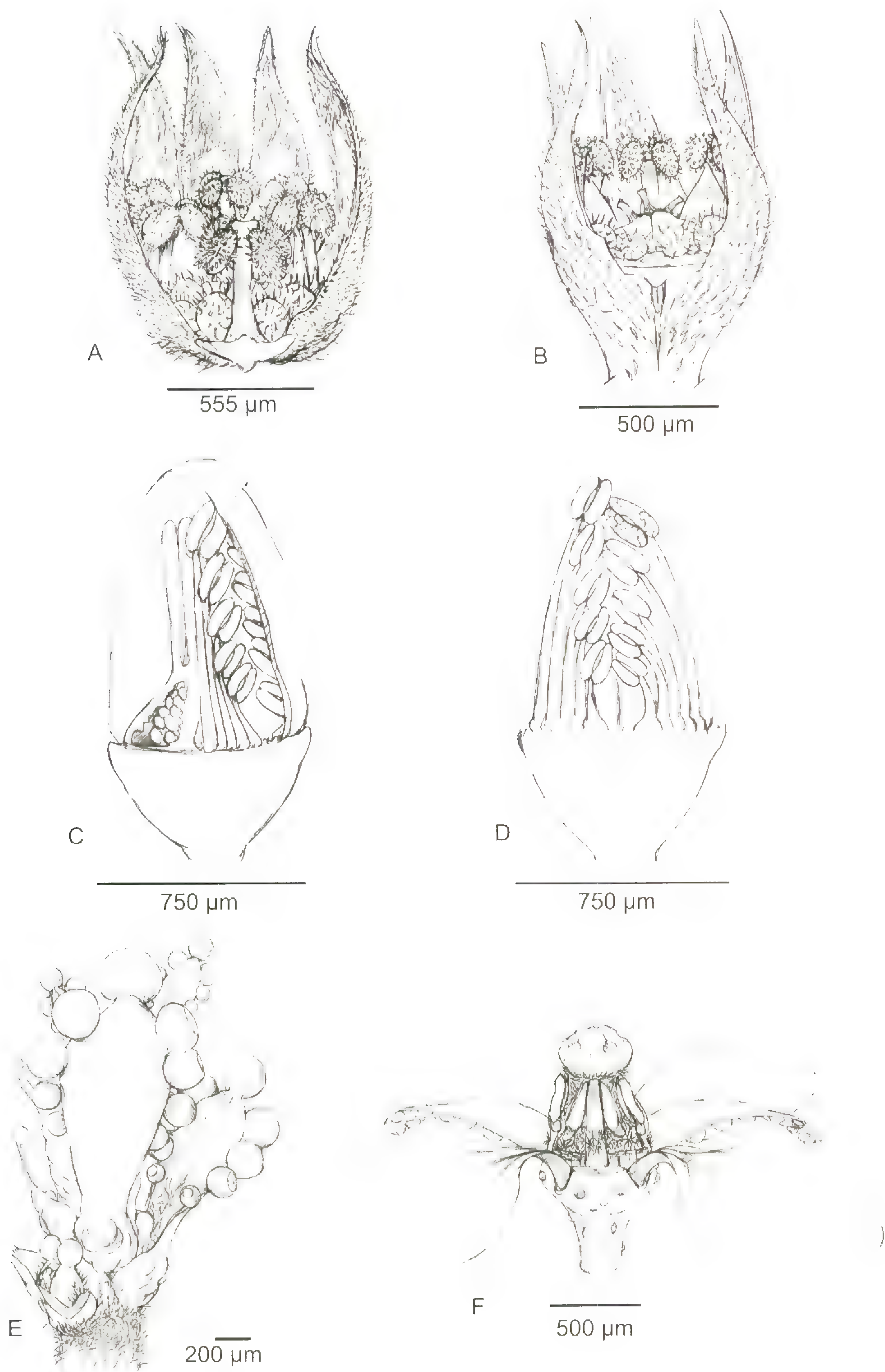


Figure 11. Reconstructions of Turonian fossil flowers with permission of Michael Rothman. A, B. Fagalean flowers. —A. Staminate floret. —B. Bisexual floret (this taxon is andromonoecious). —C, D. A generalized thealean fossil illustrating the pistil with three styles and numerous ovules and the fascicled stamens of uneven length. —E. Ericalean inflorescence with remarkable glands on the margins of the large bracts subtending paired florets, which are themselves enclosed by a pair of bracteoles, each with a terminal gland. —F. Ericalean flower reconstruction.

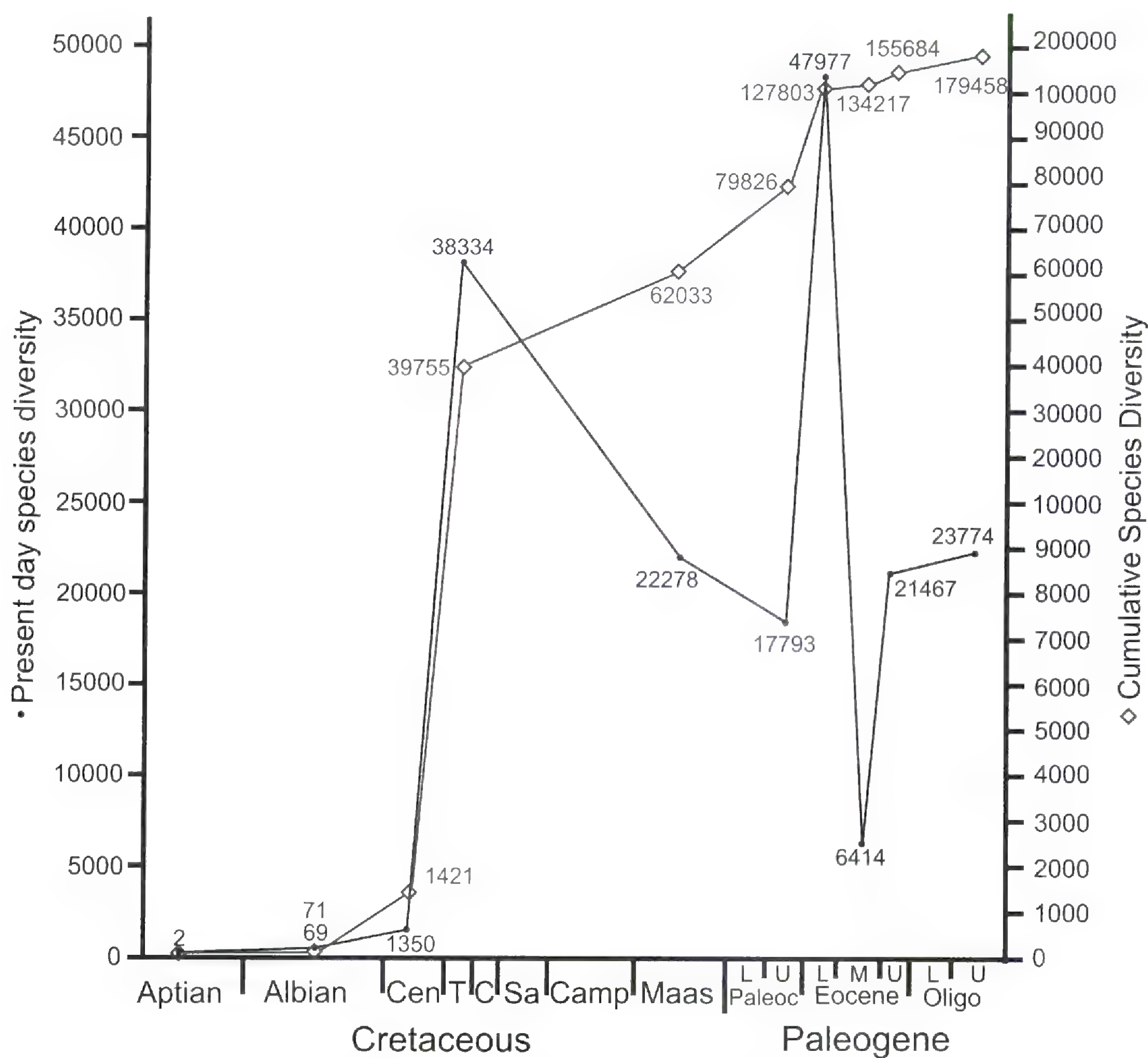


Figure 12. Cretaceous and Paleogene angiosperm species diversity through time. As has been the convention elsewhere, the relative heights of the peaks (black dots) reflect the numbers of species (y-axis scale on left) now found in angiosperm families that first occur in the fossil record at the corresponding times indicated on the x-axis. Thus, 38,334 species occur in modern families that first appear in the Turonian (see text discussion). Cumulative species diversity through time is illustrated with diamonds, according to the y-axis scale on the right side of the figure. Thus, while 38,334 species are now included in families that first appear in Turonian deposits, 39,755 species are now included in all angiosperm families that appeared by the Turonian.

Crepet (1984, 1996), Eriksson and Bremer (1992), Grimaldi (1999), and others. However, based on recent field and related studies, the relationship between pollinators (or classes of them) and speciation is as yet imperfectly understood and in need of further study before a cause-and-effect relationship can be postulated (e.g., Grant, 1994; Waser, 1998; Fenster et al., 2004). Figure 12 also illustrates that a dramatic increase in number of angiosperm species occurs from the end of the Cretaceous to the Middle Eocene. There is a drop in the rate of appearances of new families during the Upper Cretaceous (but against a background of steadily increasing species diversity; Fig. 12), which could be the result of sampling error

because there are few, if any, reported fossil localities with preserved diverse fossil flowers between the Coniacian and the Maastrichtian. However, best estimates of timing major groups based on molecular clock models (e.g., Lavin et al., 2005) or on minimum age node mapping (Crepet et al., 2004) suggest this apparent absence of many of the major diverse groups from the Upper Cretaceous implied by fossil evidence is real (Leguminosae, Asterids I, Euphorbiaceae, etc.). Thus, the question arises: What were the factors involved in the proliferation of angiosperm species in the Early Tertiary, and were they different from those involved in the initial establishment of angiosperm species dominance?

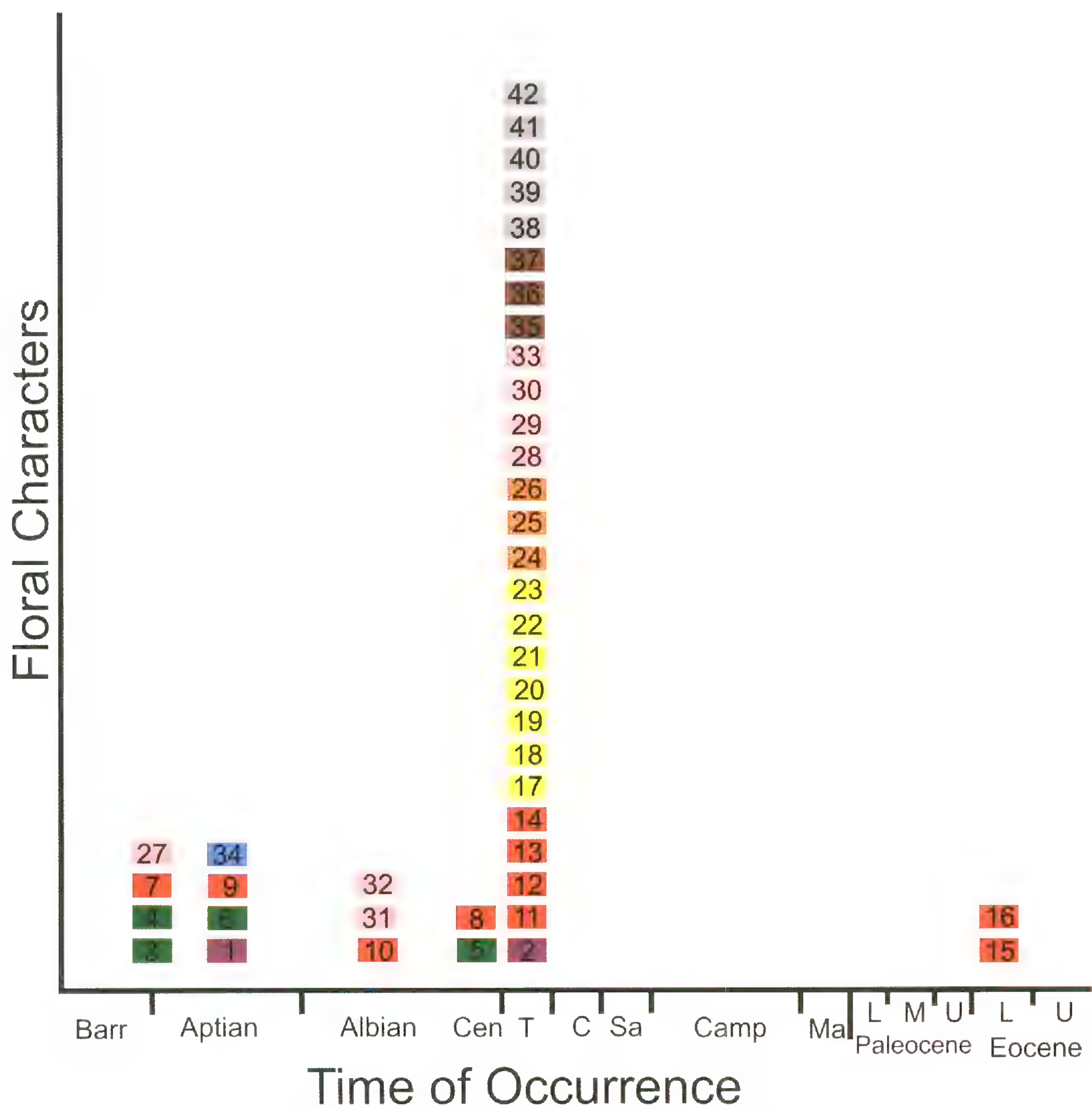


Figure 13. Times of occurrence of select floral characters. These are identified on the figure by numbers in colored boxes corresponding to the character summary below and grouped into color-coded categories (e.g., arrangement of floral parts—green) to illustrate patterns in the evolution of particular categories of floral characters. Times of appearance are noted in the summary below and illustrated on the *x*-axis of the figure. The *y*-axis illustrates numbers of characters occurring at the times indicated on the *x*-axis. **Floral receptacle** (purple). 1. Cupular (Aptian). 2. Hypanthium (Turonian). **Arrangement of floral parts** (green). 3. Paired (Barremian/Aptian). 4. Spiral (Barremian/Aptian). 5. Cyclic (Cenomanian). 6. Coalesced into “flowers” (Aptian). **Floral envelope** (red). 7. Apetaly (Barremian/Aptian). 8. Regular merosity (Cenomanian). 9. Subtending bracts/bracteoles (Aptian). 10. Numerous tepals (Albian). 11. Sepal tube (Turonian). 12. Corolla asymmetry (Turonian). 13. Clawed petals (Turonian). 14. Corolla tube (Turonian). 15. Zygomorphy (Turonian). 16. Prolonged corolla tube (Lower Eocene). **Stamens** (yellow). 17. Fascicled (Turonian). 18. Geniculate (Turonian). 19. With tubules (Turonian). 20. Dorsifixed (Turonian). 21. Inverted (Turonian). 22. Staminal tube (Turonian). 23. Staminodal nectary (Turonian). **Pollen** (orange). 24. Viscin threads (Turonian). 25. Polyads (Turonian). 26. Pantoporate pollen (Turonian). **Gynoecium** (pink). 27. Apocarpy (Barr/Aptian). 28. Inferior ovaries (Turonian). 29. Multiple carpels and elongate style (Turonian). 30. Multiple carpels and single style (Turonian). 31. Carpels fused (Albian). 32. Carpels whorled (Albian). 33. Ovary wall nectary (Turonian). **Sexuality** (blue). 34. Bisexual (perfect) (Aptian). **Reproductive condition** (brown). 35. Monoecy (Turonian). 36. Dioecy (Turonian). 37. Andromonoecy (Turonian). **Reward structure** (silver). 38. Nectar (Turonian). 39. Nectary disk (Turonian). 40. Resin (Turonian). 41. Pollen (Turonian). 42. Staminal food bodies (Turonian).

To place the Early Tertiary radiation of angiosperms in the context of earlier events in angiosperm history, early angiosperms originated and diversified in the Lower Cretaceous, enjoying some advantages over contemporary gymnosperms due to their short life cycles, self-incompatibility systems, biosynthetically diverse secondary compounds, probable insect pollination, and possibly wider ecophysiological tolerances

(e.g., Doyle, 1978; Verdú, 2002; Feild et al., 2004) and possibly because of hybrid necrosis (although its phylogenetic distribution in angiosperms has yet to be determined, making it difficult to assess its impact on angiosperm radiation; Bomblies & Weigel, 2007). Toward the Middle Cretaceous, Cenomanian deposits include the first evidence of the regular eudicot flower with distinct corolla and, in evolutionary context, what might be considered developmentally interchangeable, cyclically arranged floral parts. This floral configuration might have constituted a baseline or platform morphology that would facilitate the parsimonious origin of more advanced floral morphologies. Because many families with such derived floral morphologies are now quite diverse, the attainment of such a platform morphology in certain lineages might have catalyzed the quantum leap in angiosperm diversification that closely followed its origin as documented by angiosperms from Turonian deposits. Turonian angiosperm flowers do include those with novel morphologies and characters now associated with bee pollinators (Figs. 5G, 13). These apparently adaptive characters (Fig. 13) also occur in the same geologic timeframe as early bee pollinators, during observed increases in gross angiosperm diversity, and along with first appearances of angiosperm families that now include over 32,000 species. This broad co-occurrence of related factors suggests that the major burst of evolution accomplished in angiosperms by the Turonian supports the possibility that pollinator involvement in numerical species dominance by flowering plants cannot be ruled out based on timing alone. Yet, based on recent studies discussed above, this finding does not determine whether this co-occurrence of factors is a cause of angiosperm success or an effect of it.

Further, with respect to the second question posed above about causes of the later, but equally dramatic radiation of angiosperms in the Early Tertiary, one could ask: if flower-pollinator relationships were critical to angiosperm diversification, why, with the regular cyclic flower, bilaterality, and even the corolla tube established by Turonian times, was there an apparent lag between the Turonian and Lower Tertiary before the resumption of rapid radiation of families that was characterized by even more specific pollinator relationships associated with sometimes even more highly adapted floral structures (Fig. 7C–F)? Here, coordinated character (s.l.) evolution may make sense out of the patterns observed in the angiosperm fossil record. For example, with respect to the asterids, present since Turonian times, why do they dramatically diversify in the Tertiary and not earlier? Could the answer lie in the synergistic benefits of the co-occurrences of the apparent Tertiary

origin of the herbaceous habit in certain asterids with associated short life cycle, the floral tube (extant since the Turonian in the asterid lineage), and modes of pollination associated with it (Fig. 7F)? Could speciation-amplifying synergy be related to yet other co-occurring temporally coincident characters? Could enhancements of the speciation process postulated to be associated with specific insect pollinators combined with vertebrate seed and fruit dispersers and their possible catalysis of allopatry also account for subsequent Tertiary radiations (Crepet, 1984; Tiffney, 1986)? We don't know. Yet these possibilities are consistent with the separate angiosperm radiations observed in the fossil record. And, in the context of character evolution and its timing in angiosperm history, is it unrealistic to assume that coordinated radiations between insect pollinators and angiosperms would occur only once, especially given that the Early Tertiary radiation included taxa with zygomorphic flowers (Fig. 7E), brush flowers (Fig. 7C, D), pronouncedly elongate corolla tubes (Fig. 7F), and presumed herbaceous habits?

Thus, a better understood, more conservatively interpreted fossil record now provides details of angiosperm history that preclude eliminating the importance of insect pollinators in angiosperm diversification and instead point to its potential significance. Yet, based on available evidence from neontological investigations of pollination ecology, one cannot assume that insect pollination was the single most important factor in angiosperm radiation or really be precise in assessing its relative importance among the array of possibly important angiosperm attributes. A better way to assess relative advantages of angiospermy in the context of paleontological data might be to carefully monitor the history of individual families and to assess the possible causes for speciation patterns within those families. This approach could ultimately give us more accurate insights into causes of angiosperm numerical species dominance and is within reach of the better fossil record of angiosperms that has come from stunning advances in fossil discovery combined with precise analytical techniques that now aid in accurately identifying fossil taxa.

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